WATER MANAGEMENT EFFECTS ON PHOTOSYNTHATE DISTRIBUTION, PHYSIOLOGY, AND NUTRITIVE VALUE OF PERENNIAL PEANUT

BY

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Perennial peanut (*Arachis glabrata* Benth.) is a relatively drought tolerant tropical legume with potential for production of high quality forage on many acres of infertile and droughty soils of Florida. However, information is lacking on the response of perennial peanut to irrigation. Dry matter (DM) accumulation and distribution, single leaf carbon exchange rate (A), stomatal conductance (g), leaf and soil water status, rhizome total nonstructural carbohydrate (TNC) concentration, and nutritive value were determined on 'Florigraze' perennial peanut subjected to the following water management treatments in 1987 and 1988: 1) well-watered (WW), 2) 2-week cyclical stress (CS1), 3) 3-week cyclical stress (CS2), and 4) rainfed (RF).

Increasing severity of plant water stress caused a decrease in above-ground growth and an increase in rhizome TNC, suggesting that photosynthate was partitioned underground at the expense of above-ground

growth during periods of water deficit. Above-ground DM in the RF treatment was reduced 18 and 26% in 1987 and 1988, respectively, as compared to the average of the WW and CS1 treatments. Above-ground DM was also reduced 11% in the CS2 treatment in 1988 as compared to the WW treatment. Single leaf carbon exchange rate, *g*, and leaf water potentials were also reduced only during severe soil water deficits. On the average, *g* was reduced more than *A* during plant water stress. However, both stomatal and nonstomatal mechanisms appeared to limit *A* in perennial peanut during periods of drought. Water management had little effect on the nutritive value of perennial peanut which maintained relatively high *in vitro* organic matter digestibility and nitrogen concentration throughout both seasons.

Deep rooted characteristics of perennial peanut caused plant productivity to be insensitive to water management during relatively short periods of dry weather (2 to 3 weeks) unless soil moisture reserves deep in the profile had been depleted. Results of this study suggested that irrigation of perennial peanut would increase forage production only during periods of severe soil water deficits. During dry periods, replenishment of the soil profile with water at 2-week intervals resulted in similar forage yields to those from treatments irrigated more frequently.

INTRODUCTION

Forage production by legumes in the subtropics is often reduced by periods of drought. Extended periods with little or no rainfall are common and often limit forage productivity at times of the year when temperatures are otherwise favorable for plant growth. Since periodic loss of the above-ground portion of a forage occurs each time herbage is removed, either by livestock or by mechanical harvesting, proper management of legumes during these periods of drought is essential to provide a relatively constant amount of high quality feed. Understanding the physiological impact of drying atmospheric and soil conditions on plant growth is important to facilitate managing legumes and other forages for optimum production and nutritive value as well as plant persistence.

Perennial peanut (*Arachis glabrata* Benth.) is a deep rooted, relatively drought tolerant tropical forage legume which is well-adapted to the environmental conditions of Florida. Perennial peanut is presently being propagated on farms in Florida as the cultivars 'Florigraze' and 'Arbrook' to increase the availability of rhizomes for propagation. The cultivar Florigraze is adapted to well-drained, sandy soils and grows vigorously alone or in association with a grass (Prine et al., 1981). There is very little information available concerning the physiological response of perennial peanut to different levels of water management. Effects of drying soil on physiological processes,

photosynthate accumulation and distribution, regrowth after defoliation, and forage nutritive value are not known. Opportune applications of water may help maintain favorable plant water status for growth and increase overall forage yields through increased numbers of cuttings, more rapid regrowth, and improved crop persistence. It is important to quantify the specific physiological responses as well as whole plant responses of tropical forage legumes to drying soil conditions in order to gain a better understanding of the mechanisms impacting photoassimilate accumulation and distribution. This type of information can facilitate genetic manipulation to enhance yield and plant persistence, as well as reveal management procedures necessary to maintain vigorous stands and high forage yields throughout the growing season.

The research undertaken here examined some of the physiological, morphological, and forage quality responses of Florigraze perennial peanut to different levels of water management. The specific objectives of the study were as follows:

1) Characterize the temporal changes in photosynthate and nitrogen accumulation and distribution in response to four water management treatments.
2) Determine the responses of and relationships among leaf stomatal activity, leaf carbon exchange rate, leaf nitrogen concentration, and leaf and soil water status during water deficits.
3) Characterize the seasonal patterns of *in vitro* organic matter digestibility and nitrogen concentration of the plant and its

yield components (leaves and stems) in response to the water management treatments.

Photosynthate accumulation and distribution in a field planting of perennial peanut were monitored during two growing seasons (1987 and 1988) under four levels of water management. The effects of water management on shoot and rhizome mass were examined along with total nonstructural carbohydrate concentrations in different plant parts. Also, leaf stomatal conductance, leaf carbon exchange rate, and leaf nitrogen concentration were measured. Soil water status and leaf water potential components were characterized throughout both seasons in order to define the relationships among the plant responses and plant and soil water status. Regrowth following clipping as affected by water management was also evaluated in terms of stem numbers, rate of stem appearance, and canopy height during one season (1987).

LITERATURE REVIEW

Very limited information is available on the physiological, morphological and nutritive value responses of perennial peanut subjected to water deficits; therefore, most of the information presented in this section was compiled from research conducted on other forage and row crops.

Photosynthate Distribution in Plants

Nonstructural carbohydrate root and crown reserves as well as the presence of photosynthetically active tissue are important for forage regrowth and maintenance. Smith (1962) studied root reserves in birdsfoot trefoil (*Lotus corniculatus* L.), alfalfa (*Medicago sativa* L.), and red clover (*Trifolium pratense* L.) under several cutting treatments. He observed that root reserves were maintained at a relatively high level in alfalfa and red clover under three and two harvests, respectively, per season as well as in the uncut treatment. Birdsfoot trefoil maintained relatively low concentrations of root reserves throughout the season across all cutting treatments until fall. Such results suggest that trefoil depends on current photosynthesis from existing leaf area in order to regrow and persist throughout the season. Similar results have been obtained by Beardsley and Anderson (1960) who compared alfalfa and trefoil. They found that birdsfoot trefoil could withstand frequent but not complete defoliation, and that alfalfa could withstand complete defoliation but on a relatively infrequent cutting

schedule so that nonstructural carbohydrate reserves could be restored during the regrowth period. Nelson and Smith (1968) also observed higher carbohydrate root reserves in alfalfa than in birdsfoot trefoil. During most of the season alfalfa had a higher crop growth rate, produced more dry matter, and had a higher leaf area index than trefoil. Feltner and Massengale (1965) studied the summer reduction in growth of alfalfa and found that day/night temperatures affected accumulation of soluble carbohydrates in the roots and that the reserves were reduced by frequent cutting. Chatterton et al. (1977) reported that alfalfa clones tolerant to relatively frequent clipping were also the clones highest in soluble carbohydrate root reserves. Maintenance of sufficient carbohydrate root reserves and/or residual light intercepting foliage after defoliation is important for rapid regrowth and crop persistence of forage legumes.

Periods of drought stress may also affect the partitioning of photosynthate. In forage plants, the above-ground portion of the plant is of primary agronomic importance and drought may lower the amount of foliage produced either by stimulating root growth at the expense of the shoot, by stimulating leaf senescence, or by causing an overall reduction in plant growth (shoots and roots). Finn and Brun (1980) and Silvius et al. (1977) both found that in drought stressed soybean (*Glycine max* L.) more ^{14}C was partitioned to the roots at the expense of the leaves than in the unstressed plants. However, Robertson et al. (1980) reported that total root length and distribution in annual peanut (*Arachis hypogaea* L.) was unaffected by water management on a fine sand

in Florida although pod yields increased with increasing amounts of irrigation.

Nonstructural carbohydrate concentrations in various organs of the plant can be used as an indicator of the temporal distribution of photosynthate. Saldivar (1983) observed that soluble carbohydrate concentrations in perennial peanut rhizomes were higher in a "dry" year than in a "normal" year, although soil water status was not monitored during the study. He also found that within a season, rhizome soluble carbohydrate concentrations decreased during the hot, summer months but increased in the fall and were relatively high in the spring. Saldivar (1983) speculated that since growth was slower during the cooler parts of the season, demands made on the reserves were not as great thus allowing them to accumulate.

In a preliminary study of perennial peanut with and without irrigation, it was found that forage yield was depressed 45% under the nonirrigated treatment but canopy photosynthesis in the water-stressed plots was 90% of that in the well-watered plots (Albrecht et al., 1989). They also observed a 25% increase in total nonstructural carbohydrate concentration in the rhizomes of the water-stressed plants compared to well-watered plants indicating that carbon assimilated under water stress was accumulated underground in rhizomes rather than utilized for shoot growth (K.A. Albrecht, personal communication). Hall et al. (1988) reported similar results for alfalfa. Water-stressed alfalfa had greater nonstructural carbohydrate concentrations in the roots as compared to well-watered plants apparently due to increased photoassimilate partitioning to the roots during water stress.

Assimilate partitioning may also be related to the water status of the plant tissue receiving the assimilate. Lang and Thorpe (1986) showed that bathing the roots of young *Phaseolus* plants in solutions of different osmolarity caused assimilate to be distributed toward areas of more negative water potential. However, Robinson et al. (1983) studied assimilate distribution in *Gladiolus* and found that even a slight water deficit caused a decrease of assimilate deposition in the inflorescence and increased deposition of assimilates in the corm. The corm had consistently higher water potential than the inflorescence under water stress. They proposed that since turgor dependent growth was slowed in the inflorescence, more photosynthate was partitioned to the corm, allowing it to continue growth. Schulze (1986b) reviewed whole-plant responses to drought and stated that plant water relations interact with carbon partitioning, but the mechanisms controlling the interaction are obscure. He further proposed that the internal water status of a plant probably does not affect carbon assimilation and distribution extensively unless the plant fails to maintain water flow through the leaf epidermis and root tip.

Physiological Responses to Water Deficits

Plants use different strategies when responding to drought and certainly plant species differ in their ability to cope with water stress. Plants usually respond by some mechanism which allows them to maintain favorable water status needed for growth or survival under drying atmospheric and soil conditions.

Effect of Water Deficits on Stomata and Leaf Carbon Exchange

Plants respond to water deficits by decreasing stomatal aperture. Stomatal closure is usually related to drying soil conditions and has been commonly related to changes in leaf water status. However, recent evidence strongly suggests that the mechanism by which stomata respond to water deficits is not entirely understood. Bates and Hall (1981) and Osonubi (1985) found stomatal closure in cowpea (*Vigna unguiculata* L.) to be associated with changes in soil water status rather than bulk leaf water status. Blackman and Davies (1985) have also shown a direct effect of soil water status (without changes in leaf water status) on stomatal conductance in a split root experiment with maize (*Zea mays* L.). Turner et al. (1985) examined the relationship between stomatal conductance, transpiration and photosynthetic rate as related to leaf water potential in sunflower (*Helianthus annuus* L.) but found no unique relationship. Only when about two-thirds of the extractable soil water had been depleted did stomatal conductance and net photosynthesis decline, indicating that soil water status, not leaf water status, was the dominant effect on stomatal behavior and photosynthesis.

Bennett et al. (1987), working with field grown soybean and maize, examined the response of stomatal conductance to leaf water potential, leaf turgor potential and relative water content. No significant relationships were found when data for well-irrigated and mildly stressed plants were analyzed; however, when data from the more severely stressed plants were included in the analysis there were significant relationships. Such data indicate that initial stomatal response was not related to leaf water status. Carter and Sheaffer (1983a,b) studied

the effect of water stress on alfalfa and found stomatal conductance to be lower at midday and higher in the morning and late afternoon in plants under moderate water stress. However, with severe water stress, stomatal conductance was low all day and canopy temperature was up to 8.5 °C higher than for well-watered plants, indicating that stomatal closure had significantly reduced transpiration. Sharratt et al. (1983) reported a 0.2 mm h^{-1} reduction in evapotranspiration, a 0.7 MPa reduction in leaf water potential, and a 2 °C canopy temperature increase in alfalfa when extractable soil water had declined to 25% in a water-stressed treatment.

Muchow et al. (1986) examined changes in stomatal conductance as well as leaf area development and leaf N content of field-grown soybean in response to soil water deficits imposed after canopy closure. Mild water deficits were found to decrease leaf area development more than number of leaves produced. Biomass accumulation efficiency was decreased; however, interception of photosynthetically active radiation was unaffected. The relative decrease in biomass accumulation was associated with lowered stomatal conductance of the leaves in response to drying soil. Schulze (1986a), in a review on carbon dioxide and water vapor exchange in response to drought in the atmosphere and in the soil, suggested that stomata may respond in three ways to drought: 1) a direct response of stomata to humidity that is a property of the epidermis, 2) a direct response from root "signals" that are related to root metabolic activity in a drying soil, and 3) a response to leaf apoplastic abscisic acid (ABA) released to the guard cells through some unknown process that could be related to the first two.

Abscisic acid is now thought to be the principal hormone actually controlling stomatal action. Zhang et al. (1987), using a split root system with *Commelina communis* (L.), found that as the soil dried there was an increased level of ABA in leaf epidermal tissue which coincided with increased levels found in roots located in dry soil. Such results led them to conclude that ABA, which controlled leaf stomatal response, apparently originated in the roots. However, Munns and King (1988) found that ABA was not the only stomatal inhibitor present in the transpiration stream of water-stressed wheat (*Triticum aestivum* L.). Even after extracting ABA from plant exudate by passing it through an immunoaffinity column, the exudate still caused stomatal closure when "fed" to detached leaves from nonstressed wheat plants.

Leaf carbon exchange is usually reduced as stomata close when plants are subjected to drought. Silvius et al. (1977) examined drought-stressed soybeans and reported that carbon exchange rate (CER) was decreased as stomatal resistance increased, but that CER increased to prestressed levels upon rewatering if leaf water potential did not decline below -2.1 MPa. However, when leaf water potential declined below -2.1 MPa, CER did not fully recover. Albrecht et al. (1984) also reported decreased canopy CER in soybeans with increased soil drying. Upon rewatering, stomatal conductance and leaf water potential returned to normal, but canopy CER remained below the control rate. They attributed such results primarily to the abscission of leaves during stress and thus a reduction in leaf area and photosynthetic capacity, or possibly to reduced carbon fixation capacity of the recovered leaves. Nagarajah and Schulze (1983) found that carbon assimilation of cowpea

decreased less rapidly than stomatal conductance as the soil dried, and that leaf growth continued even though stomata began to close when available soil water was depleted by 45%. Küppers et al. (1988) examined the relationship between stomatal conductance and intercellular CO_2 concentration (*Ci*) in cowpea. No unique relationship between *Ci* or the ratio of ambient CO_2 concentration (*Ca*) to *Ci* and stomatal conductance was found. As the soil dried, leaf carbon exchange rate was affected less than stomatal conductance. They concluded that stomatal conductance and leaf photosynthesis responded independently. Lopez et al. (1988) found similar results for pigeonpea (*Cajanus cajan* L.) and concluded that stomatal conductance was more sensitive to water stress than leaf photosynthesis. Nicolodi et al. (1988) compared irrigated and nonirrigated alfalfa and found a lower discrimination against ^{13}C in the nonirrigated treatment indicating a reduction in CO_2 diffusion into the leaf. However, they also found that reduced photosynthesis could not always be attributed to reduced stomatal conductance. The ratio *Ci/Ca* was actually higher in water-stressed plants on several occasions indicating that a nonstomatal mechanism (ie. reduced photosynthetic capacity of the mesophyll) was contributing to reduced photosynthesis in water-stressed alfalfa. They concluded that both stomatal and nonstomatal mechanisms contributed equally to reduced photosynthesis in droughted alfalfa.

Whole Plant Responses

Several studies have been conducted to examine the response of tropical forage species to water deficits. Wilson et al. (1980) compared three tropical grasses and the tropical legume siratro

(*Macroptilium atropurpureum*) in a semi-arid field environment. The grass species were shown to adjust osmotically while siratro did not. Fisher and Ludlow (1982) also studied the water relations and adaptive characteristics of siratro under dry tropical conditions. They found that siratro maintained favorable leaf water status and avoided plant water deficits by three main mechanisms: 1) sensitive stomatal control of water loss, 2) paraheliotropic leaf movements to minimize radiation received, and 3) abscission of leaves to reduce transpiring tissue. However, they concluded that although those mechanisms allow siratro to temporarily avoid severe leaf water deficits, it cannot withstand very negative leaf water potentials which would make it susceptible to extended dry periods.

Ludlow et al. (1983) compared siratro to several *Centrosema* species, and found that unlike siratro the *Centrosema* species do adjust osmotically in order to maintain leaf turgor. Shackel and Hall (1983) also found species differences when comparing sorghum (*Sorghum bicolor* L. Moench) and cowpea under field conditions. Sorghum was shown to tolerate leaf water deficits through osmotic adjustment, whereas cowpea possessed an avoidance mechanism by maintaining favorable leaf water status mainly thorough stomatal control and deep rooting but did not osmotically adjust. Sherriff and Ludlow (1984) studied buffel grass (*Cenchrus ciliaris* L.) and siratro in a mixed sward under drought stress and found that siratro had a deeper root system than buffel grass, and buffel grass had lower daily mean water potentials than siratro. They concluded that buffel grass survived drought because of its inherent desiccation tolerance (osmotic adjustment), whereas siratro was able to

survive because it had deeper roots and was not competing with buffel grass for water.

Sheriff et al. (1986) studied the physiological responses of two forage legumes of similar morphology, siratro and *Galactia striata*, under drought and found that rooting depth and hydraulic conductance of the plant-soil system were as important as leaf physiological responses in their adaptation to drought. Siratro maintained higher leaf water potentials than *G. striata* but showed no osmotic adjustment. Even though calculated turgor was higher in siratro, leaf expansion was more affected by drought than in *G. striata*. They speculated that this may have been due to higher partitioning of assimilates to roots at the expense of leaves in siratro. The maintenance of higher leaf conductance and carbon exchange in siratro as drought progressed was attributed to its relatively deep root system. Cortes and Sinclair (1986) found similar results when comparing two soybean cultivars that differed in their response to drought. The cultivar least affected by drought developed a deeper root system under water stress thus maintaining a supply of water to plant tissues. Markhart (1985) also compared the relatively drought tolerant tepary bean (*Phaseolus acutifolius* Gray) with common bean (*P. vulgaris* L.) and found that tepary bean had more sensitive stomatal control of water loss and deeper roots than common bean.

It has been speculated that annual peanut may possess unique physiological traits that enhance its ability to grow under drought conditions. However, Bhagsari et al. (1976) found that photosynthesis in water-stressed annual peanut was controlled in a manner similar to

that in other crop species. Bennett et al. (1981, 1984) also observed that the relationships among leaf water potential components, stomatal resistance, and leaf water content were similar in peanut as in other agronomic crops and the relationships observed probably conferred no unique drought resistance mechanisms to peanut. They concluded that the ability of peanut to maintain favorable tissue water status by extracting water deep in the soil profile and its ability to maintain developmental plasticity (indeterminate growth habit) may allow sensitive growth processes to escape temporary water deficits.

Certain plant characteristics can be of direct benefit in enabling crops to withstand water deficits; however, the direct benefit of some other mechanisms that allow plants to tolerate or escape water deficits is not always clear. Sinclair and Ludlow (1986) examined the water balance of four tropical grain legumes during a soil drying cycle. They found differences in dehydration tolerance among the four legumes based on relative water content and ranked them as follows: pigeonpea > cowpea > mungbean (*Vigna mungo* L.) > soybean. The ranking based on epidermal conductance was the inverse; ie., soybean > mungbean > cowpea > pigeonpea, indicating that low epidermal conductance of pigeonpea helped the plant retard tissue desiccation thus giving it an adaptive advantage in order to withstand temporary soil water deficits. Such mechanisms would likely be of benefit only under severe water deficits, but might be important for crop survival under those environments. McCree and Richardson (1987) studied the effect of water stress on carbon gain in cowpea and sugarbeet (*Beta vulgaris* L.) plants. Cowpea tended to avoid leaf water deficits through stomatal closure and water regulation. In

contrast, sugarbeet allowed stomata to remain open through osmotic adjustment, theoretically giving it a carbon gain advantage. However, they found similar carbon gains for the two species under the same environmental conditions and concluded that there was no advantage of osmotic adjustment over stomatal closure in plant response to soil water deficits.

Effect of Water Stress on Forage Nutritive Value

Water deficits frequently affect the nutritive value of forages. Drought stress usually causes an increase in digestibility of alfalfa due to shorter internodes which result in decreased stem to leaf ratios in the stressed forage (Brown and Tanner, 1983; Carter and Sheaffer, 1983a; Jensen et al., 1988). Plant crude protein concentration is generally only slightly affected by water stress; however, Donovan and Meek (1983) found that the protein concentration of alfalfa was higher in the spring and fall under dry as compared to well-irrigated conditions.

Conflicting results concerning the effect of water-stress on forage digestibility exist in the literature. Wilson (1983b) examined three tropical grasses subjected to water deficits and found that both stem and leaf digestibility were similar to or higher than those from unstressed herbage. However, Pitman et al. (1981, 1983) reported a decrease in forage quality associated with drought in tropical grasses as did Wilson (1983a) with the perennial legume siratro. Pitman et al. (1983) found that in water-stressed Kleingrass (*Panicum coloratum* L.) an increased proportion of cell wall components and increased lignification could account for at least part of the decreased digestibility

associated with water stress. Wilson and Ng (1975) also found decreased cell wall digestibility with increasing water stress in *Panicum maximum* var. *trichoglume*. Pitman and Holt (1982) studied the effects of temperature, rainfall, relative humidity and daylength on three perennial, warm season grasses in the Southwest but found only poor relationships between these environmental factors and forage digestibility.

It has also been speculated that physiological maturity may play a role in accounting for differences detected in forage nutritive value under water stress. Wilson (1983a) observed that dry weather in the spring slowed stem development of the three grasses tested and reported that digestibility was significantly higher than in the well-irrigated treatment. Halim et al. (1989) studied water stress effects on alfalfa forage nutritive value after adjusting for maturity differences, but found that maturity differences among water treatments accounted for only part of the differences.

Much research has focused on only one or two aspects of the many physiological processes impacting on forage management decisions during drought. Many experiments have examined stomatal control factors and photosynthesis, mostly in temperate forages and other agronomic crops, with limited information available for tropical legumes. Also, characterization of nonstructural carbohydrate distribution in forages (mostly temperate species) has been done in response to cutting height and frequency but not to drought. No relationships between these intimately related parameters have been examined on tropical species which are void of sexually reproductive sinks. The tropical nature and

lack of a seed sink in species such as perennial peanut may influence assimilate accumulation, partitioning and remobilization, as well as plant productivity, senescence, and persistence.

In two reviews on crop water deficits and plant adaptations to stress, Turner (1986a,b) points out the need to more fully understand the complex relationships that exist between leaf stomatal response, root water relations, and drying soil conditions. Plant roots seem to mediate the relationships by chemical and/or hydraulic responses to dry soil. Once these relationships begin to be characterized and understood then the possibility for beneficial genetic manipulation exists (Boyer, 1982). Definitive trait(s) need to be identified which can be selected for and incorporated into germplasm through breeding programs to make crop plants better adapted to varying environments (Turner, 1986b).

MATERIALS AND METHODS

This study was conducted at the Irrigation Research and Education Park located on the Agronomy Farm at the University of Florida in Gainesville. The experimental site was on a Kendrick fine sand (a member of the loamy, siliceous, hyperthermic family of Arenic Paleudults), a deep, well-drained to excessively well-drained soil.

Establishment of Perennial Peanut (1986)

Soil test results at the initiation of the study indicated a pH of 5.5 to 6.0, relatively high levels of available phosphorous, and low available potassium. A preplant application of 730 kg ha^{-1} of 0-5-25 (N-P_2O_5-K_2O) containing 70, 8, 5, 2, and 91 g kg^{-1} of the micronutrients Mg, Mn, Zn, B, and S, respectively, was made in November 1985. On 4 February and 19 March 1986, pelletized dolomitic limestone was applied at the rate of 1000 kg ha^{-1}. A fall maintenance application of 220 kg ha^{-1} of 0-0-61 (N-P_2O_5-K_2O) fertilizer was also applied on 24 Sep. 1986 after establishment of the crop.

Perennial peanut cv. 'Florigraze' rhizome material, which had been inoculated with peanut Bradyrhizobium at 25 kg ha^{-1}, was planted on 30 and 31 January 1986, in 15 cm rows at the rate of 8.7 m^3 ha^{-1}. To encourage rapid establishment of the crop, a total of 198 mm of water was applied to all plots during 1986 with 114 mm being applied in April and May. Rainfall and irrigation amounts are shown in Table A-1. Weeds were controlled with appropriate herbicide treatments and by hand-

weeding during the 1986 season. 'Premerge' (dinoseb, 2-sec butyl 4,6-dinitrophenol) and 'Lasso' (alachlor, 2-chloro-2'-6'-diethyl-N-(methoxymethyl)acetanilide) were applied on 19 March for preemergence control of annual grasses and broadleaf weeds. 'Fusilade' (fluazifop-butyl, butyl(RS)-2-[4-[[5-(trifluoromethyl)-2-pyridinyl]oxy]phenoxy] propanoate) was applied on 2 May for post-emergence grassy weed control, and yellow nutsedge (*Cyperus esculentus* L.) was controlled with two post-emergence applications of 'Basagran' (bentazon, 3-isopropyl-1H-2,1,3-benzothiadiazin-(4)-3H-one 2,2-dioxide) on 23 June and 22 July. By the end of July, solid rows of vigorous plants had developed, and abundant rhizomes were detected spreading underground between the rows. All plots were cut to a 5-cm stubble height for the first time after planting on 30 July in anticipation that removal of shoot apical meristems would promote sprouting from rhizomes. Subsequent sprouting did occur from rhizomes, and plants began to cover the row middles. Six plots were harvested to a 5-cm stubble height on 31 October to estimate establishment season forage yields. Forage dry matter yields for each harvested area and the mean yield are given in Table A-2.

Treatments and Data Collection (1987 and 1988)

Four water management treatments replicated three times were imposed during the study, resulting in a total of 12 plots situated within an existing 0.25-ha field area which was equipped with a solid set irrigation system. The plots were arranged in a randomized complete block design with blocking based on depth of soil to the underlying clay layer. Depth of soil to the clay layer ranged from 950-1050 mm in block 1 to 1200-1300 mm in block 3. Each plot measured 13.7 x 6.9 m. All

data were analyzed using analysis of variance and Duncan's New Multiple Range test available through Statistical Analysis System (SAS Institute, 1985).

Maintenance fertilizer applications of 220 kg ha^{-1} of 0-0-61 (N-P_2O_5-K_2O) were applied on 4 April and 22 June 1987; and on 12 February and 14 April 1988. Weeds were controlled during the 1987 and 1988 seasons principally by hand-weeding although several herbicides were also utilized. Fusilade was applied on 10 July 1987 for postemergence grassy weed control, mainly common bermudagrass (*Cynodon dactylon* L.). In 1988, early season broadleaf weeds were controlled postemergence with '2,4-D' (2,4-Dichlorophenoxyacetic acid) applied on 1 March, and summer annual grassy and broadleaf weeds were controlled with a preemergence application of 'Prowl' (N-(1-ethylpropyl)3,4-dimethyl-2,6-dinitro benzenamine) on 4 March.

Water Management Treatments

Four water management treatments were imposed on perennial peanut in both 1987 and 1988. In 1987, the treatments were as follows: 1) well-watered (WW), irrigated so that plants were never subjected to plant water deficits; 2) cyclical stress (CS1) with periodic water recharge of the soil profile; 3) water withheld until stomata began to close, then light frequent irrigation to replenish daily evapotranspiration (SP); and 4) rainfed (RF). Treatment WW received 19 mm of water every 2 to 4 days as needed during periods of dry weather throughout the growing season. The CS1 treatment received 38 to 45 mm of water at approximately 10-day intervals to provide complete soil water recharge during the first harvest cycle which ended on 11 June.

For the remainder of the season, soil water recharge for the CS1 treatment was every 2 weeks during periods of dry weather. As part of another study which was corollary to the study reported herein, a Speedling irrigation system was used to apply daily replacement of evapotranspiration on the SP treatment only during the first harvest cycle (treatment no. 3). For purposes of the corollary study, daily midday measurements of stomatal conductance (*g*) were made on the WW, SP, and RF treatments during the first harvest cycle (25 April through 11 June). Light, frequent irrigation (often times daily) was used to maintain *g* in the SP treatment at a level intermediate to the WW and RF treatments. This treatment was suspended after the first cycle, and thereafter received the same irrigation as the CS1 treatment during the rest of the season. The RF treatment was only irrigated to initiate uniform crop growth in April and was never irrigated after that time. Rainfall and irrigation data are summarized in Table A-3 for the 1987 growing season.

Water management treatments in 1988 were as follows: 1) well-watered (WW), received approximately 19 mm of irrigation every 2 to 4 days during periods without significant rainfall; 2) 2-week cyclical stress (CS1), received approximately 38 to 46 mm irrigation to achieve complete soil water recharge every 14 days during periods without rainfall; 3) 3-week cyclical stress (CS2), received approximately 38 mm of water to achieve complete soil water recharge every 21 days during periods without rainfall; and 4) rainfed (RF), no irrigation. The water management treatments were the same in both years except for treatment no. 3. The SP treatment of 1987 was not repeated in 1988 due to data

which suggested this treatment did not differ from the WW treatment during the first harvest cycle in 1987. Since the SP treatment was assumed similar to both the WW and CS1 treatments at the end of 1987 (data presented in following sections), replacement of the SP treatment with a 3-week cyclical stress treatment in 1988 was considered to be a better use of resources. Table A-4 presents rainfall and irrigation data for the 1988 growing season.

Gravimetric Soil Water Content

Gravimetric soil water content was monitored at the end of several cyclical stress periods in order to assess the soil water deficits created by the imposed water management treatments. Soil core samples were taken on 31 May, 10 June and 30 Oct. 1987; and on 2 and 8 June, and 2 Nov. 1988. Soil samples were extracted at various soil depths by utilizing a 5-cm diameter aluminum tube. Samples were collected at 150-mm depth increments to a total depth of 1200 mm or until encountering the clay layer. The soil samples were sealed in plastic bags until wet soil weight could be determined in the laboratory. After weighing, the bags were opened and the samples were dried at 95°C in a forced air oven for at least 24 h. Percent water in the soil was calculated on a dry weight basis as follows:

% gravimetric soil moisture = ((wet wt. - dry wt.)/dry wt.) * 100.

Determination of Crop Dry Matter Accumulation and Distribution

Temporal changes in photosynthate distribution as influenced by water management were monitored throughout the growing seasons in 1987 and 1988 by measuring shoot and rhizome dry matter (DM) as well as total nonstructural carbohydrate (TNC) distribution in stems, leaves, and

rhizomes. On sampling dates, two 0.5 m^2 quadrats from each plot were clipped to ground level to determine above-ground DM, and four soil core samples (9.5 cm in diameter) were extracted to a depth of 20 cm from each quadrat to determine rhizome DM. Soil samples were placed on a fine screen and washed with a high pressure water stream from a spray nozzle to separate rhizomes from the soil. Total nonstructural carbohydrate concentrations were determined on the subsamples of leaf, stem, and rhizome tissue.

Beltranena (1980) found that the highest seasonal forage DM yields of Florigraze perennial peanut were obtained at 6 and 8 week cutting intervals in 1978 and 1979, respectively. However, seasonal forage yields were reduced at 2 and 4 week clipping intervals. Based on those data, four harvest cycles of 6 to 7 week intervals were utilized during both years of the study. In 1987, above-ground and rhizome samples were taken on 15 May, 1 June, 11 June (end of first harvest cycle), 23 July (end of second harvest cycle), 8 September (end of third harvest cycle), and 2 November (end of fourth harvest cycle). In addition to samples for total DM (clipped to ground level), forage samples (harvested from an area 0.86 x 3.05 m clipped to a 5-cm stubble height in order to estimate forage available for grazing) were taken on all dates except 15 May.

Total above-ground and rhizome DM samples were taken in 1988 on 19 May, 2 June, 8 June (end of first harvest cycle), 25 July (end of second harvest cycle), 12 September (end of third harvest cycle), and 1 November (end of fourth harvest cycle). Forage samples in 1988 were harvested as previously described at the end of each harvest cycle

except for the 1 November sampling date when insufficient plant material was available for harvesting. All plots were staged (clipped) to a 5-cm stubble height at the end of each harvest cycle and clipped forage was removed from the plot area.

Subsamples were taken from the above-ground DM samples to determine leaf and stem fractions, as well as leaf area index of the crop at the time of harvest. Fresh subsamples were also taken from the forage samples in the field. All plant samples were dried at least 72 h at 60°C in forced-air ovens before determining dry weights. Subsamples and rhizome samples were then ground to pass a 1-mm screen and subjected to various laboratory analyses (see section on laboratory analyses).

Root length density expressed as cm root per cm^3 soil was measured on 19 June 1987. The modified line intersect method of estimating root length as described by Tennant (1975) was utilized to determine root length. Two 5-cm diameter soil cores were collected at 150-mm depth increments to a total depth of 1200 mm. Rhizomes were separated from the 0-150 mm increment, and their length was determined and reported independently from roots at that depth.

Determination of Crop Regrowth After Clipping

Regrowth from the staging height of 5 cm was monitored in 220 cm^2 areas at two locations in each plot and described in terms of shoot origin (rhizome or stubble) and shoot number, plant height, and light interception during both the second (12 June - 23 July) and the third (24 July - 8 September) harvest cycles in 1987.

Physiological Measurements

Single leaf carbon exchange rate (A), stomatal conductance, and transpiration were determined with a LI-COR 6200 Portable Photosynthesis System equipped with a 0.25-l chamber during periods of water stress in the spring and fall. Two pairs of leaflets from two different locations in each plot were measured periodically at midday as plant water deficits developed in the different treatments. Fully illuminated, recently expanded leaves at the top of the canopy were selected for measurement. Two of the four leaflets were removed to facilitate insertion and positioning of the two remaining leaflets in the leaf chamber. Measurements were taken on 18, 26 and 29 May; 8 and 10 June; 27 and 28 August; and 7, 22 and 29 October during 1987. In 1988 measurements were taken on 12, 16, 20 and 31 May; 1 June; 8 July; and 17 and 24 October. Carbon exchange data were always taken under full sun between 1030 and 1500 h EST.

Plant water potential was also monitored during periods of plant water stress on 8 and 10 June, 28 August, and 29 October in 1987; and on 1 June and 8 July in 1988. Two to four leaflets were collected from each plot and quickly enclosed in thermocouple psychrometer chambers. The psychrometers were transferred to the laboratory and placed into a thermostatically controlled water bath at 30°C and allowed to equilibrate for 4 hours. A dewpoint microvoltmeter was utilized to pass a 15 s cooling current through the thermocouple and to monitor output from the psychrometers. The output was recorded with a chart recorder and data taken from the output chart were used to calculate total leaf water potential (ψ_L) of each sample. Each psychrometer had been

previously calibrated using known concentrations of NaCl solutions to develop a regression equation of water potential versus psychrometer output. After ψ_L determination, psychrometer units containing leaf material were placed in a freezer at -20°C for at least 12 h to rupture the cells and eliminate cell turgor. After removal from the freezer, tissue was re-equilibrated in the water bath at 30°C, and osmotic potential (ψ_π) was determined by the method previously described. Leaf turgor (ψ_P) was calculated by subtracting ψ_π from ψ_L.

Leaf Carbon Exchange Rate and Leaf Nitrogen Concentration

Leaflets of Florigraze perennial peanut from the WW and CS1 treatments on which *A* had been measured were collected, dried and pooled together according to the rate of *A*. Pooled leaflets were ground to pass a 1 mm screen and then analyzed for nitrogen (N) concentration. It was necessary to pool several leaflets to obtain adequate leaf mass for N determination because of their small size. Leaflets from 1987 and 1988 were kept separate. Six intervals of *A* were chosen to group leaflets of similar carbon exchange rates for N analysis as follows: 1) *A* less than or equal to 14 μmols CO_2 m^{-2} s^{-1}, 2) *A* from 15 to 17 μmols CO_2 m^{-2} s^{-1}, 3) *A* from 18 to 20 μmols CO_2 m^{-2} s^{-1}, 4) *A* from 21 to 23 μmols CO_2 m^{-2} s^{-1}, 5) *A* from 24 to 26 μmols CO_2 m^{-2} s^{-1}, and 6) *A* greater than or equal to 27 μmols CO_2 m^{-2} s^{-1}. Such pooling of leaflets provided enough leaf mass in 1987 to analyze one sample for N concentration at each of the levels 2 through 6 in the WW treatment; and 1, 3, 4, 5, and 6 for the CS1 treatment. In 1988 sufficient plant material was collected to analyze one sample for N concentration from each of the levels 1 through 5 for the WW treatment, and 2 through 4 for the CS1 treatment.

Therefore, a total of 18 composite leaflet samples were obtained for N analysis on the cultivar Florigraze.

An establishing stand of well-watered 'Arbrook' perennial peanut was also utilized in order to obtain leaflets of varying carbon exchange rates corresponding to varying leaf N concentrations. Arbrook perennial peanut rhizomes were planted in March 1988 in plots adjoining the Florigraze cultivar, and fertilizer N treatment (with and without ammonium nitrate) was imposed as a split-plot feature in each plot. Nitrogen was applied three times in 1988 at the rate of 78, 67 and 61 kg ha^{-1} on 26 May, 6 July and 3 August, respectively. Plant leaves from the no N fertilizer plots had a pale green ("yellow") color as compared to leaves on plants that received fertilizer N. Two fully expanded "yellow" and "green" leaflets at the top of the canopy from the no N and N fertilized plots, respectively, were used to measure *A* utilizing the LI-COR 6200 Portable Photosynthesis System as previously described. Two to three leaflet pairs in each sub-plot were subjected to measurement and collected on 17, 22, 23, and 24 June; 7, 8, 13 and 15 July; and 2, 18 and 29 August. Leaflets of similar carbon exchange rates were pooled together for N analysis as previously described for the Florigraze cultivar. Samples from June, July and August were kept separate, and "yellow" and "green" leaflets were pooled independently of each other. In June, "yellow" and "green" leaflets were obtained for N analysis at each of the levels 1 through 5 (as described above), and 3 through 6, respectively. In July, "yellow" and "green" leaflets were grouped into each of the levels 1 through 5, and 1 through 6, respectively; and leaflets from August into each of the levels 4 through 6 for both

"yellow" and "green". Therefore, a total of 26 composite Arbrook leaflet samples were obtained for N analysis.

Laboratory Analyses

Total nonstructural carbohydrate and N concentrations were determined on leaf and stem components of above-ground DM subsamples as well as on rhizome DM subsamples. Nitrogen concentrations were also determined on the forage subsamples and composite samples of leaflets used for measurement of *A*. Total nonstructural carbohydrate analyses were performed by enzymatic digestion according to procedures described by Christiansen (1982) in which nonstructural carbohydrate components (ie. starch and sucrose) were digested to glucose, with subsequent colorimetric determination of glucose. The data were compared to a standard curve which was developed for each individual set of samples in order to quantify the amount of TNC present. For N analysis, samples were digested using a modification of the Kjeldahl aluminum block digestion procedure of Gallaher et al. (1975). Ammonia in the digestate was determined by semiautomated colorimetry (Hambleton, 1977).

Leaf and stem fractions of the above-ground DM subsamples and the forage subsamples were also analyzed for *in vitro* digestion. *In vitro* organic matter digestibility (IVOMD) was determined by the two-stage technique of *in vitro* digestion (Tilley and Terry, 1963) as modified by Moore and Mott (1974).

RESULTS AND DISCUSSION

Rainfall and Irrigation Amounts and Distribution

1987 Season

Rainfall in 1987 totalled 1156 mm which was similar to the 30-year mean of 1338 mm (Table 1). The early part of the year (January through March, before water management treatments were imposed) was wetter than normal. However, as is typical for this region, several dry periods occurred during the growing season from late May to late June, mid August to mid-September and in the month of October (Fig. 1 and Table 1). Rainfall was only 56% of the 30-year average during the initial growing period and first two harvest cycles (April through July), and October was exceptionally dry. After mid-September to the end of the last harvest cycle (2 November) there was no significant rainfall (only 10 mm from 20 September and 1 November). This dry period of 41 days caused perennial peanut to exhibit severe plant water stress symptoms by the end of October. In general, rainfall distribution during 1987 was typical of most years with adequate rainfall during the mid summer and dry periods during the spring and fall. However, the drier than normal spring and fall in 1987 would be expected to amplify any responses to irrigation observed in this study compared to those which might be expected in normal years.

Rainfall and irrigation data specific to each of the four harvest cycles are summarized in Table 2. Specific dates and amounts of

Table 1. Monthly rainfall for 1987 and 30-year mean monthly rainfall for Gainesville, Florida.

Month	Rainfall	
	1987	30-year mean
	----------mm----------	
January	106	83
February	138	100
March	261	93
April	11	74
May	108	106
June	75	167
July	99	176
August	137	204
September	93	143
October	7	59
November	109	51
December	30	82
Total	1156	1338

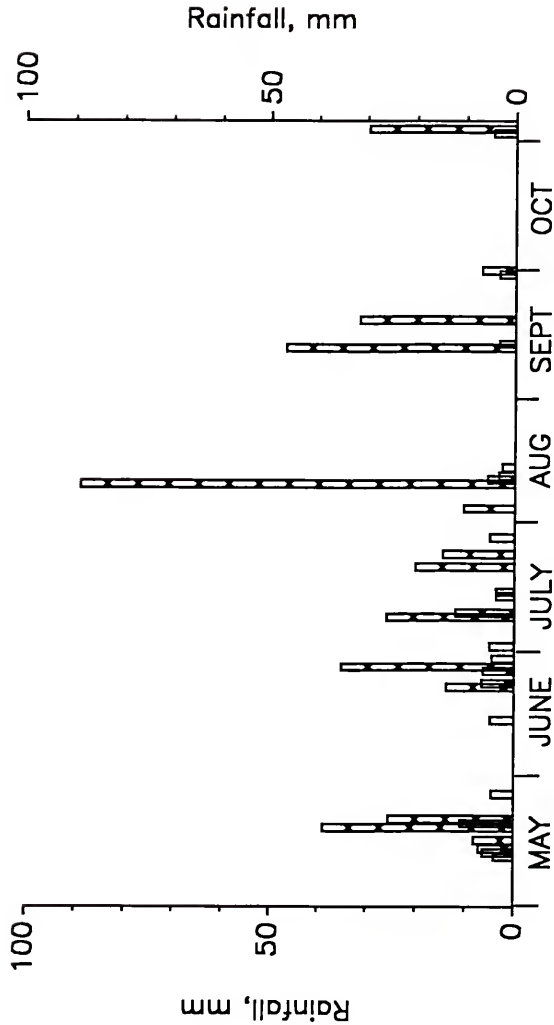

Figure 1. Daily rainfall distribution during the growing season for perennial peanut in 1987 at Gainesville, Florida.

Table 2. Rainfall and irrigation specific to each harvest cycle as well as before and after the perennial peanut growing season in 1987.

Interval of time	Dates	Rainfall	Irrigation treatments†			
			WW	SP	CS1	RF
		mm				
Pre-treatment	1 Jan. - 24 Apr.	517	93	93	93	93
Harvest cycle 1	25 Apr. - 11 June	110	346	89	127	-
Harvest cycle 2	12 June - 23 July	152	64	38	38	-
Harvest cycle 3	24 July - 8 Sep.	144	160	32	32	-
Harvest cycle 4	9 Sep. - 2 Nov.	94	98	57	57	-
After final harvest	3 Nov. - 31 Dec.	139	-	-	-	-
	Total	1156	761	309	347	93

†Abbreviations are as follows: WW) well-watered, SP) speedling, CS1) cyclical-stress 1, RF) rainfed.

rainfall received and irrigation applied to each water management treatment are given in Table A-3. Because of limited amount and poor distribution of rainfall in harvest cycles 1 and 3, relatively large amounts of irrigation were applied (346 and 160 mm, respectively) to the WW treatment (Table 2). More rainfall and better distribution resulted in less irrigation in mid summer (harvest cycle 2). Total irrigation was 761, 309, 347 and 93 mm for the WW, SP, CS1 and RF treatments, respectively, over the entire growing season. However, only 89 mm of water was actually applied to the SP treatment utilizing the Speedling irrigation system during the time that the treatment was active (25 April to 11 June 1987). Following termination of the early-season SP treatment, the CS1 and SP treatments were irrigated together and subjected to a total of four complete 2-week cyclical stress periods during the remainder of the season. The WW treatment received more irrigation than the other treatments during each harvest cycle since it was irrigated rather frequently in order to avoid the development of plant-water deficits during the season.

1988 Season

Total rainfall of 1558 mm in 1988 was again similar to the 30-year mean rainfall of 1338 mm (Table 3). Several dry periods occurred throughout the growing season in May, June, the first part of July, and October (Fig. 2 and Table 3). Similar to 1987, rainfall in 1988 was 57% below the 30-year mean during the period April through July (Table 3). No irrigation was applied pretreatment to initiate uniform growth as had been done in 1987. Rather, the four water management treatments were continued beginning with early season growth. Plants in the water-

Table 3. Monthly rainfall for 1988 and 30-year mean monthly rainfall for Gainesville, Florida.

Month	Rainfall	
	1988	30-year mean
	----------mm----------	
January	131	83
February	122	100
March	198	93
April	35	74
May	82	106
June	84	167
July	98	176
August	378	204
September	283	143
October	32	59
November	81	51
December	34	82
Total	1558	1338

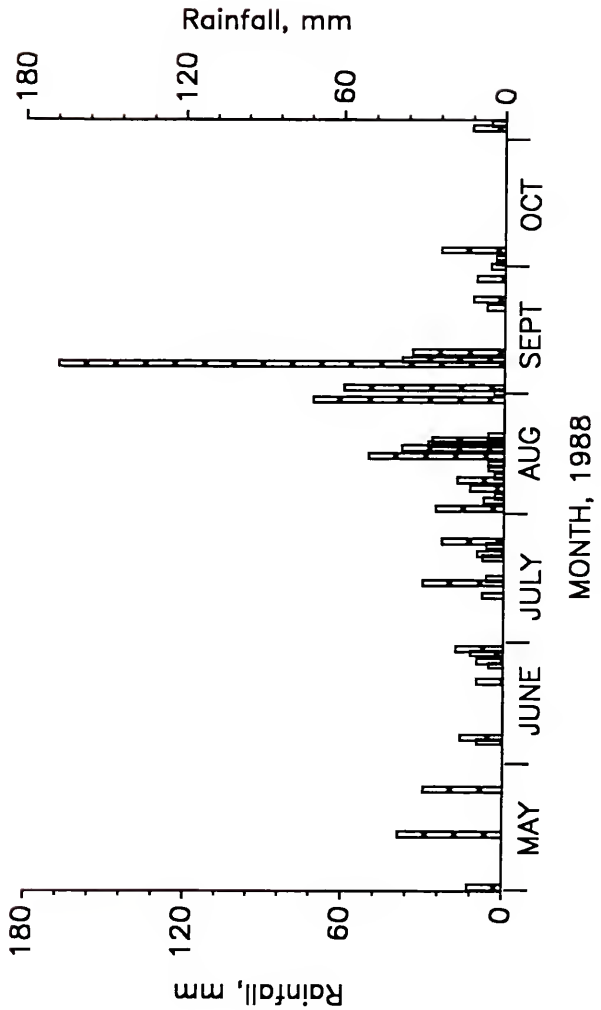

Figure 2. Daily rainfall distribution during the growing season for perennial peanut in 1988 at Gainesville, Florida.

stressed treatments showed visual symptoms of plant water stress in the first harvest cycle during periods without rainfall. Above average rainfall occurred in August and September, while October was quite dry. Even though there was a 28-day period in October without rainfall during the last harvest cycle, 32 mm of rainfall were received from 1 to 4 October (Figure 3). Moreover, average night temperature in October was 4.5°C below the normal with temperatures dropping below 10°C on 12 occasions and to 5.5°C on four occasions. Visible symptoms of plant water stress never became apparent during the 28-day dry period at the end of the season in 1988, and lower than average night temperatures likely limited growth on all treatments during October more than did water management. Again, rainfall distribution for 1988 was quite typical with dry conditions occurring in the spring and fall, and abundant rainfall occurring in the summer.

Table 4 summarizes the irrigation and rainfall amounts specific to each harvest cycle in 1988. Specific dates and amounts of rainfall received and irrigation applied to each water management treatment are given in Table A-4. A relatively large amount of irrigation was applied to the WW and CS1 treatments during the first harvest cycle because of limited rainfall (Table 4). Even though rainfall was below average during the second harvest cycle, fairly uniform distribution (except during mid June and early July) precluded the need for large amounts of irrigation during this time. Abundant rainfall was received during the third harvest cycle. Even though the last four weeks of the fourth harvest cycle were dry, cool fall temperatures precluded the need to irrigate as frequently as was done during hot, dry periods in the late

Table 4. Rainfall and irrigation specific to each harvest cycle as well as before and after the perennial peanut growing season in 1988.

Interval of time	Dates	Rainfall	Irrigation treatments†			
			WW	CS1	CS2	RF
		mm				
Pre-treatment	1 Jan. - 28 Mar.	449	-	-	-	-
Harvest cycle 1	29 Mar. - 8 June	144	201	139	44	-
Harvest cycle 2	9 June - 25 July	153	96	46	38	-
Harvest cycle 3	26 July - 12 Sep.	625	34	-	-	-
Harvest cycle 4	13 Sep. - 1 Nov.	72	99	36	38	-
After final harvest	2 Nov. - 31 Dec.	115	-	-	-	-
	Total	1558	430	221	120	-

†Abbreviations are as follows: WW) well-watered, SP) speedling, CS1) cyclical-stress 1, RF) rainfed.

spring and summer. Total irrigation applied in 1988 was 430, 221, 120, and 0 mm in the WW, CS1, CS2, and RF treatments, respectively. Again the WW treatment received more water than the other treatments, and less irrigation was applied as severity of water-stress treatment increased. The CS1 and CS2 treatments were subjected to five and three complete cycles of stress, respectively, during 1988. These complete cycles were limited to the spring and fall periods. As was the case in 1987, the below normal rainfall in spring and summer would be expected to amplify the responses to irrigation observed in this study compared to that which might occur with more normal rainfall patterns.

Rainfall amounts and distributions observed in 1987 and 1988 were fairly typical of those common to North Florida and, if anything, would result in greater than normal responses to supplemental irrigation, especially during the spring and fall months. Results from this study would therefore seem appropriate to provide information on the response of perennial peanut to water management in typical or slightly drier than normal production years.

Photosynthate Accumulation and Distribution

1987 Season

Above-ground DM production during the 1987 growing season as well as the effect of water management on DM accumulation is shown in Figure 3. As is typical of warm season plants, perennial peanut produced most of its above-ground growth during the late spring and hot summer months, with declining production in the fall. Water management had only minimal effects on above-ground DM accumulation during the 1987 season. Even though there were drying conditions in late May and early June,

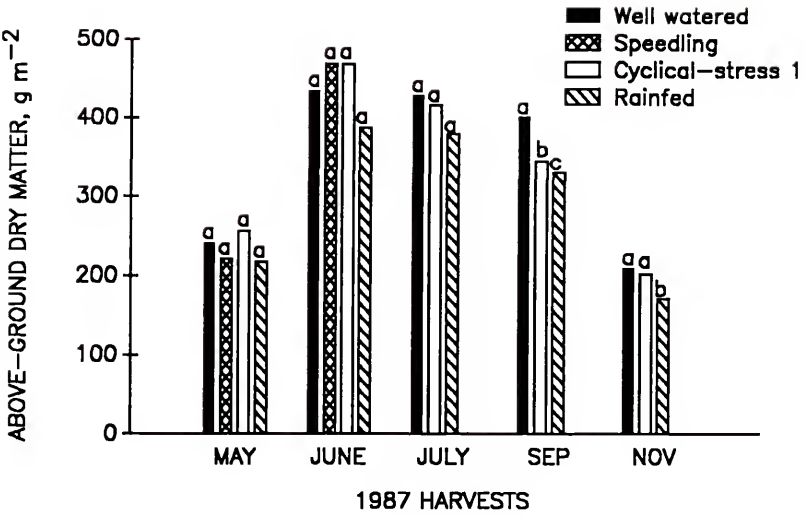

Figure 3. Above-ground dry matter accumulation of perennial peanut as affected by water management treatment on 15 May, 11 June, 23 July, 8 Sep., and 2 Nov. 1987. Different letters above bars within a harvest date indicate differences at $P \leq 0.05$ according to Duncan's New Multiple Range Test.

they had no effects on above-ground DM accumulation. The absence of a response to irrigation during the spring and early summer may have been due to above-average rainfall early in the year (January through March) as well as pretreatment irrigations that were applied in April to initiate uniform growth in all plots. As a result, soil water was plentiful at the beginning of the imposition of the water management treatments.

Another dry period from mid August to early September significantly reduced above-ground DM accumulation during the third harvest cycle (24 July - 8 September) in both the CS1 and RF treatments (Fig. 3, September harvest). Between mid September and the end of the growing season there was an extended dry period of 41 days without significant rainfall which also caused a reduction in above-ground DM accumulation in the RF treatment during the last harvest cycle (9 September - 2 November). However, above-ground DM was minimal at the end of the fall harvest cycle and the reduction in the RF treatment actually represented only a relatively small amount of available forage.

Table 5 shows numerical data for above-ground DM as illustrated in Figure 3 as well as total, rhizome, and forage DM distribution and leaf area index (LAI) for each harvest. Except for slight effects on above-ground DM accumulation in the fall, water management treatments imposed in 1987 had little effect on total DM or rhizome DM present on any given sampling date (Table 5). Water management had no effect on DM accumulation and distribution or LAI at the 15 May and 1 and 11 June harvest dates. On 11 June, at the end of the first harvest cycle, there was a tendency for more DM to occur in the rhizomes and less to occur

Table 5. Above-ground, rhizome, total, and forage dry matter distribution and leaf area index (LAI) of perennial peanut as affected by water management treatments in 1987.

Harvest date†	Water management treatment	Dry Matter				LAI
		Above-ground	Rhizome	Total	Forage‡	
		----------g m^{-2}----------				
15 May	Well-watered	241 a*	528 a	769 a	-	2.7 a
	Speedling	221 a	704 a	925 a	-	2.4 a
	Cyclical-stress 1	256 a	594 a	850 a	-	2.7 a
	Rainfed	217 a	492 a	710 a	-	2.2 a
1 June	Well-watered	419 a	564 a	983 a	276 a	4.3 a
	Speedling	396 a	572 a	968 a	264 a	4.1 a
	Cyclical-stress 1	403 a	630 a	1033 a	268 a	4.3 a
	Rainfed	372 a	666 a	1037 a	244 a	3.9 a
11 June	Well-watered	435 a	578 a	1013 a	323 a	4.7 a
	Speedling	469 a	683 a	1152 a	292 a	4.8 a
	Cyclical-stress 1	468 a	692 a	1160 a	328 a	4.8 a
	Rainfed	387 a	813 a	1200 a	249 a	4.0 a
23 July	Well-watered	429 a	592 a	1021 a	338 a	4.4 a
	Cyclical stress 1	416 a	627 a	1043 a	315 a	4.3 a
	Rainfed	379 a	564 a	943 a	295 a	4.0 a
8 September	Well-watered	402 a	746 a	1148 a	303 a	4.0 a
	Cyclical stress 1	344 b	790 a	1134 a	235 ab	3.5 b
	Rainfed	330 c	710 a	1040 a	184 b	3.5 b
2 November	Well-watered	210 a	1089 a	1299 a	25 a	1.9 a
	Cyclical stress 1	202 a	1054 a	1256 a	25 a	1.8 a
	Rainfed	171 b	1075 a	1249 a	15 a	1.3 a

† Since plots were not staged until 11 June, the data obtained on 15 May, 1 June, and 11 June represent cumulative growth. In contrast, above-ground data for 23 July, 8 September, and 2 November represent only accumulation during each respective harvest cycle. Rhizome dry matter data represent cumulative growth throughout the growing season.

‡ Represents dry matter above 5-cm cutting height.

* Means within a column on each harvest date followed by the same letter do not differ at $P \leq 0.05$ as determined by Duncan's New Multiple Range test.

above-ground in the RF treatment as compared to the other three treatments; however, total DM accumulation was not different among any of the treatments. As expected, total DM present increased in each water management treatment throughout the first harvest cycle (ended 11 June). Periods of dry weather that occurred during rapid growth in late spring had no effect on the growth of the crop. Leaf area index increased steadily from an average of 2.5 on 15 May (approximately halfway through the first harvest cycle) to a relatively high value of 4.6 by 11 June. Average forage yield taken at that time was approximately 300 g m^{-2} which compares favorably to expected first cutting yields of alfalfa in Florida (Romero et al. 1987) and yields collected from first cuttings of perennial peanut by Beltranena (1980).

Root samples taken on 19 June (after the first harvest cycle) indicated no differences in root proliferation and distribution due to the water management treatments imposed during the dry, spring period (Fig. 4). All treatments had roots deep in the profile and roots up to 5 mm in diameter were found in all plots penetrating into the underlying clay layer at the 1050 to 1200 mm depth. Deep rooting characteristics along with rainfall that occurred apparently allowed plants in the RF treatment to avoid severe water stress during the spring. It is unfortunate that the heavy clay layer below 1200 mm prevented accurate sampling of roots deeper in the soil profile.

Water management also did not affect DM accumulation and distribution or LAI at the end of the second harvest cycle on 23 July, but there was again a tendency for the RF treatment to have less above-ground DM than the other treatments (Table 5). Regrowth was also

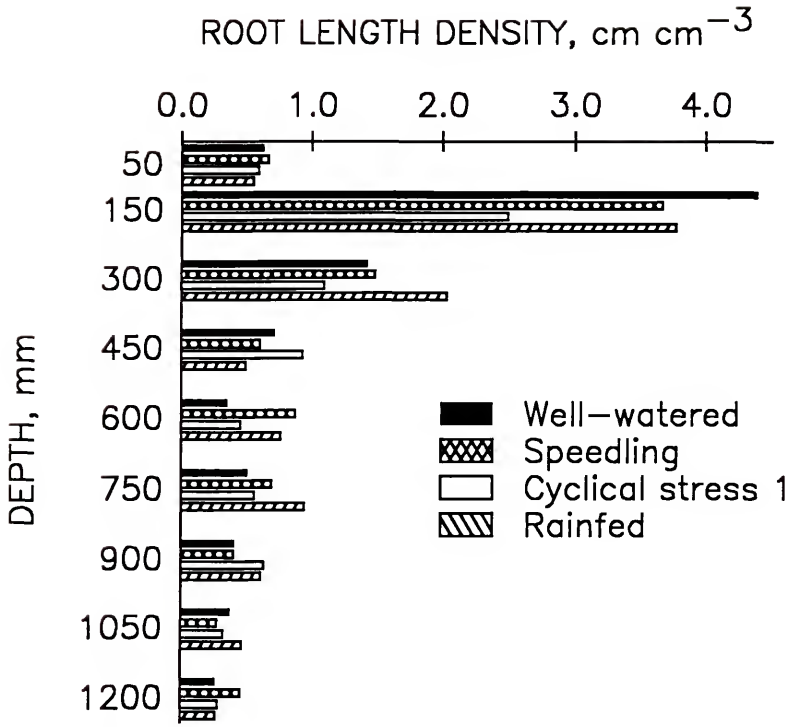

Figure 4. Root length density of perennial peanut as affected by water management treatment on 19 June 1987. Root length density of rhizomes is reported separately at the 50-mm depth since they occur as a rhizome mat just beneath the soil surface.

monitored during the second harvest cycle. Water management had no effect on number or origin of shoots, light interception, or plant height during regrowth. On the average, there were 15 stubble units (stems 5 cm tall from previous staging) per 100 cm^2 of ground area. Stubble units produced the most shoots during regrowth with rhizomes only giving rise to four shoots per 100 cm^2 of ground area by the end of the harvest cycle (23 July). The balance of new shoots originated from basal stem buds of the stubble. Since this was a first attempt at monitoring regrowth, a final count of all shoots originating from the stubble units was not done. However, in the subsequent regrowth period (third harvest cycle) each stubble unit produced two or three new shoots. Averaged across water management treatments, light interception increased from 62% on 1 July (20 days after staging) to 85% on 8 July and to 97% on 22 July. Final plant height averaged 17 cm on 23 July.

As previously mentioned, water management did have an effect on above-ground DM at the end of the third harvest cycle on 8 September (Table 5). Above-ground DM was reduced 14 and 18% in the CS1 and RF treatments, respectively, as compared to the WW treatment. Forage yield was 39% lower in the RF treatment as compared to the WW treatment, and LAI was reduced 12% by the CS1 and RF treatments as compared to the WW treatment. Parameters monitored with respect to regrowth were only slightly affected by water management. Stubble again averaged 15 units per 100 cm^2 throughout the harvest cycle and overall plant height was unaffected by water management even though above-ground DM and LAI had been reduced in the CS1 and RF treatments. New shoots originating from rhizomes showed a significant reduction on 5 September as a result of

water stress, being reduced from 4 stems per 100 cm^2 in the WW treatment to 1 stem per 100 cm^2 in the CS1 and RF treatments; however, shoots arising from rhizomes only accounted for an average of 5% of the total shoots present at the end of the harvest cycle, indicating that most regrowth of perennial peanut after clipping occurred from basal stem buds. Therefore, this procedure was not pursued as a method of quantifying the effect(s) of previous or current plant water stress on growth of perennial peanut. Reductions in above-ground DM and LAI were more sensitive indicators of the effects of plant water stress than shoot numbers, shoot origin, or plant height. Light interception was inconclusive in this study because of the difficulty involved in positioning a light sensing bar below the leaf canopy. The relatively low staging height of 5 cm in this study led to the development of leaves below that point, and it was often impossible to position the light sensor at the bottom of the canopy without grossly disturbing it.

After the 8 September harvest, little above-ground DM accumulated during the rest of the season (Table 5). Plants only attained heights of 6 to 8 cm during this harvest cycle in all water management treatments. At the 2 November harvest, above-ground DM was reduced 17% in the RF treatment as compared to the average of the WW and CS1 treatments. However, average forage yield was negligible at 22 g m^2 as a result of the short plant height, and LAI was also low (<2.0) for all treatments.

On the average, rhizomes comprised most of the total DM that was present at any given time throughout the growing season (Fig. 5 and Table 5). During rapid, above-ground growth (June and July harvest

cycles), the proportion of rhizome DM declined; however, it later increased to a very high value at the November harvest date. Averaged across water management treatments, rhizome DM constituted approximately two-thirds of the total DM throughout the season except in the fall (2 November) when rhizome DM was 85% of total DM. Rhizome DM increased 43% during the last harvest cycle, actually causing total DM to be at its maximum value for the entire season. During this time, most photoassimilate was apparently partitioned to rhizomes (underground) at the expense of above-ground growth; therefore, forage DM accumulated during the last harvest cycle was very small.

Total nonstructural carbohydrate accumulation and distribution were also monitored in rhizomes throughout the season. In general, rhizome TNC declined during the hot, summer months and increased again in the fall (Fig. 6). Changes in rhizome TNC would suggest that perennial peanut relied less on rhizome carbohydrate reserves for spring and early summer growth, but more so during the hot summer months, at which time rapid above-ground growth of the crop occurred. In the fall, photoassimilate partitioning was directed to the underground rhizomes. A similar seasonal distribution pattern of rhizome TNC has been shown by Saldivar (1983).

Water management had no effect on TNC accumulation or distribution during the first or second harvest cycles (ended 11 June and 23 July, respectively), although the trend for slightly higher TNC in the CS1 and RF treatments as compared to the WW treatment is noticeably consistent (Fig. 6). Water stress (RF treatment) caused rhizome TNC to be 38% higher as compared to the WW treatment during the third harvest cycle

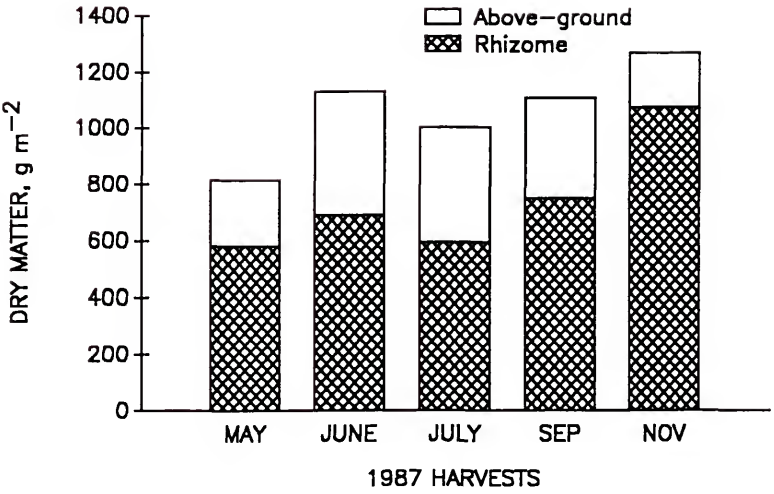

Figure 5. Above-ground, rhizome, and total dry matter of perennial peanut (averaged across all water management treatments) on 15 May, 11 June, 23 July, 8 Sep., and 2 Nov. 1987.

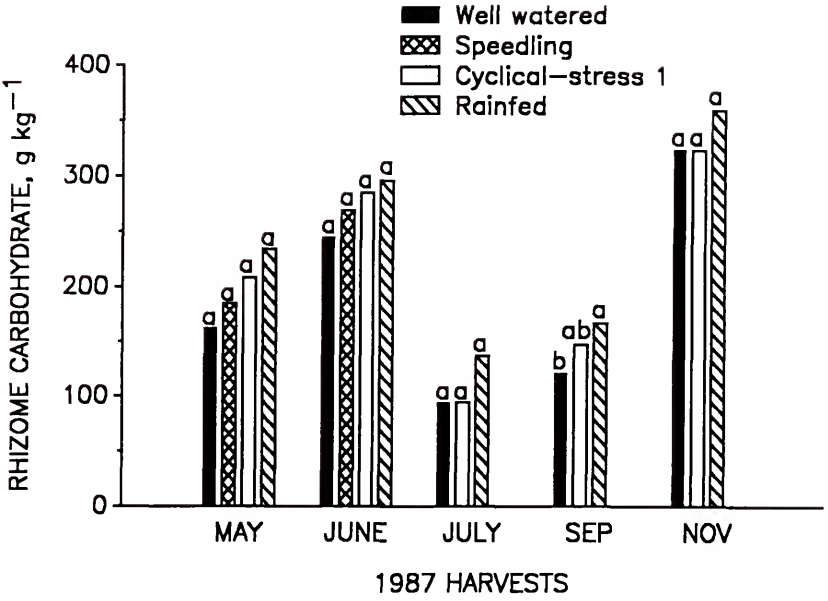

Figure 6. Rhizome nonstructural carbohydrate concentration of perennial peanut as affected by water management treatment on 15 May, 11 June, 23 July, 8 Sep., and 2 Nov. 1987. Different letters above bars within a harvest date indicate differences at $P \leq 0.05$ according to Duncan's New Multiple Range Test.

(ended 8 September). Above-ground DM had also been reduced 18% during the third harvest cycle in the RF as compared to the WW treatment, suggesting that water stress caused photoassimilate to be partitioned underground to rhizomes at the expense of above-ground growth during soil water deficits. Even though October was relatively dry and above-ground DM was reduced in the RF treatment during the last harvest cycle, no significant differences were observed in rhizome TNC on 2 November. There does, however, appear to be a trend for slightly higher TNC in the RF treatment as compared to the WW and CS1 treatments.

Total nonstructural carbohydrate concentrations in leaves and stems were fairly constant throughout the season. At no time did water management treatment affect leaf or stem TNC concentrations. Seasonal averages of TNC were 58 and 69 g kg^{-1} for the leaves and stems, respectively (Data not shown).

Photosynthate accumulation and distribution in perennial peanut was relatively unresponsive to water management in 1987. Only during periods of no appreciable rainfall for greater than two weeks did the water stress treatment(s) (CS1 and RF or RF alone) cause a reduction in above-ground DM or cause rhizome TNC to significantly increase (Figs. 3 and 6).

Averaged across water management treatments, cumulative above-ground DM production for the 1987 season was 1019 g m^{-2} (Table 6). Above-ground DM accumulation was 440 g m^{-2} through 11 June at which point all plots were staged to a 5 cm stubble height (ie., height of cut for forage sample). The above-ground DM for on 23 July (316 g m^{-2}) represents only the forage DM taken during the second harvest cycle,

Table 6. Above-ground, rhizome, total, and forage dry matter production by perennial peanut averaged across water management treatments in 1987.

Date	Dry Matter			
	Above-ground	Rhizome	Total	Forage
	----------g m^{-2}----------			
11 June	440	111†	551	298
23 July	316‡	-97	219	316
8 Sep.	241‡	154	395	241
2 Nov.	22‡	326	348	22
Cumulative total	1019	494	1513	877

† Represents average dry matter accumulation in rhizomes between the 15 May and 11 June sampling dates.

‡ Represents dry matter accumulated above the 5-cm stubble height (forage).

since the forage harvest represented all above-ground growth that had occurred above the stubble height since the 11 June staging. Likewise, above-ground DM for 8 September (241 g m^{-2}) and 2 November (22 g m^{-2}) corresponded to forage DM. Therefore, summing the above-ground DM accumulated for each harvest cycle gives a cumulative DM production of 1019 g m^{-2} for the season. Average rhizome DM present increased from 580 g m^{-2} on 15 May to 1074 g m^{-2} on 2 November, representing a net increase of 494 g m^{-2}. Summing above-ground and rhizome DM, total DM accumulated for the season was 1513 g m^{-2}. Assuming a 184-day growth period from May through October, the average daily rate of DM accumulation was computed to be 8.2 g m^{-2}. Summing forage DM accumulation from each harvest cycle gives a total of 877 g m^{-2} for seasonal forage yield. This is similar to previous seasonal forage DM yields reported by Prine et al. (1981) and Valentim (1987).

Seasonal DM accumulation and distribution for each water management treatment is shown in Table 7. Cumulative DM and seasonal forage yield for the different water treatments were not different in 1987. Nevertheless, there does appear to be a trend for lower above-ground, total, and forage DM in the RF treatment as compared to the WW treatment.

1988 Season

Seasonal distribution of above-ground DM for 1988 was similar to that of 1987 with most production occurring in the late spring and summer followed by a decline in the fall (Fig. 7). Data presented in Figure 7 also depict the effect of the four water management treatments on DM accumulation on different harvest dates. Below average rainfall

Table 7. Seasonal dry matter accumulation and distribution as affected by water management treatment in 1987.

Water management treatment	Dry Matter			
	Above-ground	Rhizome	Total	Forage
	----------g m^{-2}----------			
Well-watered	1101 a*	561 a	1662 a	990 a
Speedling	-	-	-	-
Cyclical-stress 1	1043 a	460 a	1503 a	903 a
Rainfed	882 a	585 a	1467 a	744 a

* Means within a column followed by the same letter do not differ at $P \leq 0.05$ as determined by Duncan's New Multiple Range test.

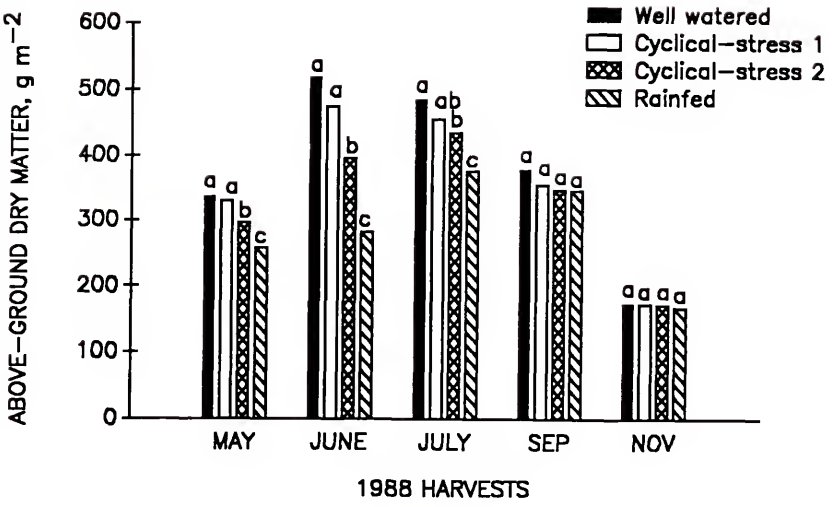

Figure 7. Above-ground dry matter accumulation of perennial peanut as affected by water management treatment on 19 May, 8 June, 25 July, 12 Sep., and 1 Nov. 1988. Different letters above bars within a harvest date indicate differences at $P \leq 0.05$ according to Duncan's New Multiple Range Test.

during the spring of 1988 caused a reduction in above-ground DM accumulation in the water stressed (CS2 and RF) treatments as compared to the WW and CS1 treatments during that time. The effect of drying conditions on the reduction of DM accumulation in the RF and CS2 treatments can be seen as early as 19 May (approximately halfway through the first harvest cycle). By the end of the first harvest cycle (8 June) above-ground DM in the RF treatment had been greatly reduced as compared to the other treatments. Another dry period in July during the second harvest cycle also had an impact on above-ground DM accumulation causing it to be reduced in the RF treatment as compared to the WW and CS1 treatments. Abundant rainfall during August and September precluded any further effects of water management during the remainder of the season. Even though there was a 28-day dry period during October, lower than average night temperatures may have limited growth more than water management during that time.

Table 8 shows numerical data for above-ground DM as illustrated in Figure 7 as well as total, rhizome, and forage DM distribution and LAI on each harvest date of the 1988 season. Water management treatment principally affected only above-ground growth and accumulation in 1988, as was the case in 1987, with little effect on rhizome and total DM. As previously mentioned, below average rainfall during the spring and early summer caused a reduction in above-ground DM accumulation in two water management treatments (CS2 and RF treatments) during May through July as compared to the WW and CS1 treatments. It is important to realize that pretreatment irrigations were not applied in 1988 to initiate uniform growth as had been done in 1987. Rather, the water management

Table 8. Above-ground, rhizome, total, and forage dry matter distribution and leaf area index (LAI) of perennial peanut as affected by water management treatments in 1988.

Harvest date†	Water management treatment	Dry Matter				LAI
		Above-ground	Rhizome	Total	Forage‡	
		g m^{-2}				
19 May	Well-watered	337 a*	937 a	1274 a	-	3.4 a
	Cyclical-stress 1	330 a	917 a	1247 a	-	3.4 a
	Cyclical-stress 2	296 b	1034 a	1330 a	-	3.1 a
	Rainfed	258 c	1087 a	1345 a	-	2.5 b
2 June	Well-watered	455 a	1059 a	1514 a	-	4.7 a
	Cyclical-stress 1	432 ab	905 a	1337 a	-	4.2 ab
	Cyclical-stress 2	384 b	1026 a	1410 a	-	3.7 b
	Rainfed	296 c	1053 a	1349 a	-	2.8 c
8 June	Well-watered	519 a	909 a	1428 a	492 a	5.2 a
	Cyclical-stress 1	475 a	1007 a	1482 a	466 a	4.6 a
	Cyclical-stress 2	396 b	985 a	1381 a	306 b	3.9 b
	Rainfed	282 c	1016 a	1298 a	191 c	2.7 c
25 July	Well-watered	486 a	599 a	1085 a	397 a	4.9 a
	Cyclical stress 1	456 ab	643 a	1099 a	360 ab	4.6 a
	Cyclical-stress 2	435 b	737 a	1172 a	349 b	4.6 a
	Rainfed	377 c	760 a	1137 a	269 c	4.3 a
12 September	Well-watered	348 a	720 a	1068 a	278 a	3.5 a
	Cyclical-stress 1	347 a	800 a	1147 a	300 a	3.9 a
	Cyclical-stress 2	356 a	702 a	1058 a	312 a	3.6 a
	Rainfed	380 a	674 a	1054 a	307 a	3.9 a
1 November	Well-watered	167 a	820 a	987 a	-	1.4 a
	Cyclical stress 1	172 a	927 a	1099 a	-	1.5 a
	Cyclical-stress 2	174 a	885 a	1059 a	-	1.5 a
	Rainfed	171 a	950 a	1121 a	-	1.6 a

† Since all plots were not staged until 8 June, the data obtained on 19 May, 2 June, and 8 June represent cumulative growth. In contrast, above-ground data for 25 July, 12 September, and 1 November represent only accumulation during each respective harvest cycle. Rhizome dry matter data represent cumulative growth throughout the growing season.

‡ Represents dry matter above 5-cm cutting height.

* Means within a column on each harvest date followed by the same letter do not differ at $P \leq 0.05$ as determined by Duncan's New Multiple Range test.

treatments were continued beginning with the initiation of spring growth. Additionally, plants in the water stress treatments had been previously subjected to water deficits in the fall of 1987. The previous stresses coupled with the dry spring period in 1988, and the fact that no pretreatment irrigation was applied all probably contributed to reduced above-ground DM accumulation in the water stress treatments during the spring.

April precipitation was 53% below normal and there were only three rainfall events in May. Water management significantly affected above-ground DM accumulation and LAI during the first harvest cycle (ended 8 June) (Table 8). The effects of plant water stress were detected midway through the first harvest cycle on 19 May with above-ground DM being reduced 11 and 23% in the CS2 and RF treatments, respectively, as compared to the average of the WW and CS1 treatments. A difference in LAI was also detected on 19 May, being 2.5 in the RF treatment and averaging 3.3 in the other three treatments. Similar differences were detected on 2 June with above-ground DM in the RF treatment being only 67% of that present as the average of the WW and CS1 treatments. The CS1 and CS2 treatments were not different on this sampling date; however, the CS2 treatment had accumulated 16% less above-ground DM as compared to the WW treatment. Leaf area continued to accumulate in the irrigated treatments more rapidly than in the RF treatment with the RF treatment remaining relatively low (2.8) on 2 June as compared to the average of the WW and CS1 treatments (4.4). In addition, a difference in specific leaf area (SLA) was detected at this sampling with leaves in

the RF treatment being thicker and having lower SLA (136 cm^2 g^{-1}) as compared to leaves in the WW treatment (148 cm^2 g^{-1}).

At the end of the first harvest cycle (8 June) above-ground DM was reduced 20 and 43% by water stress in the CS2 and RF treatments, respectively, as compared to the average of the WW and CS1 treatments. Forage yields (cut to 5 cm stubble height) were also reduced with increasing water stress (Table 8). Forage yields were drastically reduced in the RF treatment (191 g m^{-2}) as compared to the average of the WW and CS1 treatments (479 g m^{-2}). Forage DM in the CS2 treatment was also reduced 36% as compared to the average of the WW and CS1 treatments. Final LAI of perennial peanut at the end of the first harvest cycle was relatively high in the nonstressed plots at 4.9 (average of the WW and CS1 treatments) as compared to 3.9 and 2.7 in the CS2 and RF treatments, respectively. Leaves in the RF treatment were much thicker and had a lower SLA (130 cm^2 g^{-1}) as compared to the average of the WW and CS1 (149 cm^2 g^{-1}), and CS1 and CS2 (144 cm^2 g^{-1}) treatments, respectively. This is a typical response of leaves formed under conditions of plant water deficits. As was the case in 1987, no differences were detected in rhizome or total DM accumulation as affected by water treatment. However, there does appear to be a trend for reduced total DM accumulation in the CS2 and RF treatments as compared to the WW and CS1 treatments at the end of the first harvest cycle (8 June).

Gravimetric soil water content data taken at the end of the first harvest cycle on 8 June nicely illustrates differences resulting from the various water management treatments. Reduced soil water content was

observed for all water stress treatments (CS1, CS2 and RF) as compared to the WW treatment at the 150, 300, 450, 600, 750 and 1050 mm depths (Fig. 8). The entire soil profile was very dry in the RF treatment (average of 1.9%) down to the 1200 mm depth. The clay layer below this depth probably provided at least a limited amount of soil moisture to the crop in these plots (as well as in the other treatments). Soil water content was intermediate between the WW and RF treatments for the CS1 and CS2 water management treatments. As previously mentioned in the 1987 section, deep rooted characteristics of perennial peanut probably contributed to its drought tolerance during periods of up to two weeks without rainfall or irrigation.

There was an 11-day period without rainfall midway through the second harvest cycle (ended 25 July) when plants in the water stressed treatments (CS2 and RF) showed signs of drought stress (paraheliotropic leaf movements and folding of leaves). Above-ground DM was reduced in the CS2 and RF treatments as compared to the WW treatment during the second harvest cycle even though no differences in LAI were detected (Table 8). The fact that the plants in the water-stressed treatments had been under prolonged drought stress during the first harvest cycle, and below average rainfall for June and July likely contributed to the observed differences even though the dry period was relatively short. Above-ground and forage DM were reduced 20 and 29%, respectively, in the RF treatment as compared to the average of the WW and CS1 treatments.

Water management had no effect on DM accumulation and distribution, LAI, or SLA during the rest of the season (third and fourth harvest cycles which ended 12 September and 1 November,

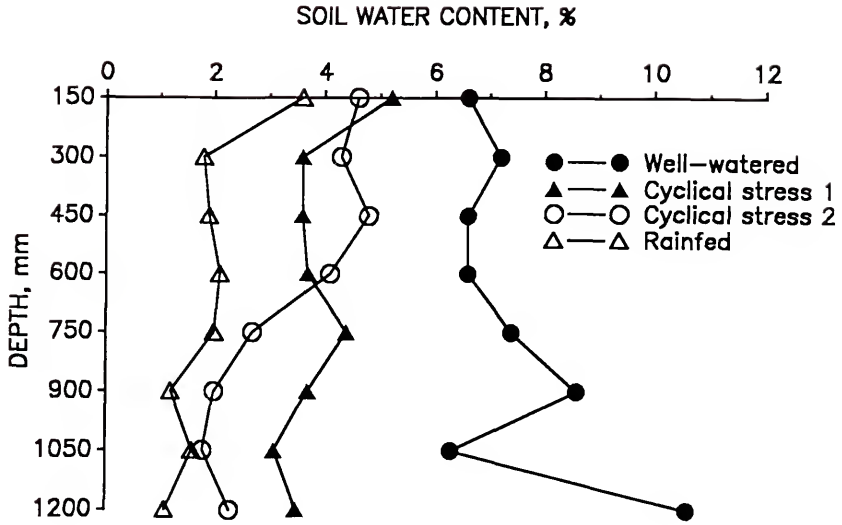

Figure 8. Gravimetric soil water content on 8 June 1988.

respectively). There was above average rainfall in August and September as well as 32 mm of rainfall during the first four days of October. Even though there was no more precipitation during the rest of October (remainder of the last harvest cycle), below normal night temperatures may have limited growth in all treatments more than did water stress during the fourth harvest cycle. Again, very little above-ground DM accumulated during the last harvest cycle as was the case in 1987. Leaf area index remained very low (averaging 1.5) at the end of the fourth harvest cycle on 1 November; however, the amount of DM present in rhizomes increased.

On average, rhizome DM constituted most of the total DM present throughout the season in 1988 as had been the case in 1987 (Fig. 9 and Table 8). During rapid above-ground growth (first and second harvest cycles), the proportion of total DM in rhizomes decreased, however it increased again during the fall. Averaged across water management treatments, rhizome DM again constituted approximately two-thirds of the total DM present during any given harvest cycle except in the fall (fourth harvest cycle ended 1 November) when rhizomes were 84% of total DM. Average DM in rhizomes increased 24% during the last harvest cycle which was somewhat less than the 1987 increase of 43% possibly because of cooler than average weather in October. Photoassimilate accumulated in rhizomes during the last harvest cycle (12 September to 1 November) at the expense of above-ground DM accumulation, and forage DM was negligible on the last harvest date because plants had remained only 5 to 6 cm tall since the previous staging on 12 September. Rhizome DM at the end of 1988 (1 November) was similar to that at the beginning of

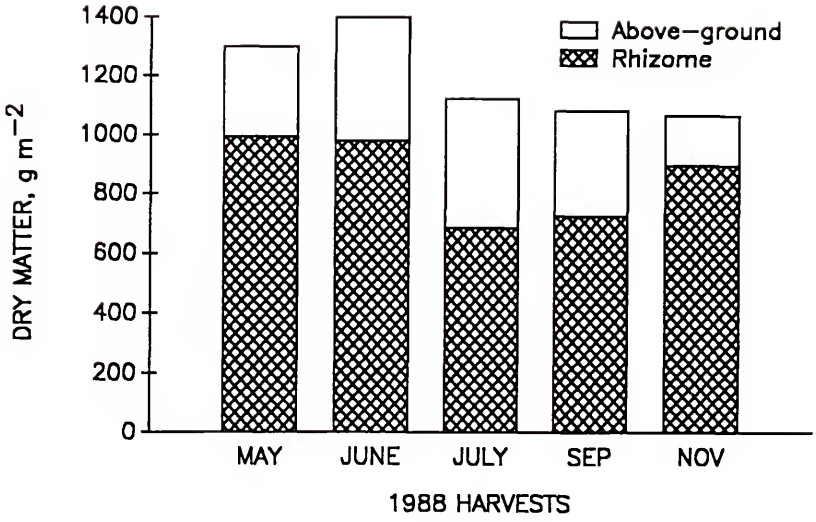

Figure 9. Above-ground, rhizome, and total dry matter of perennial peanut (averaged across all water management treatments) on 19 May, 8 June, 25 July, 12 Sep., and 1 Nov. 1988.

1988 (19 May). This is in contrast to the large increase in rhizome DM observed during the 1987 growing season (see Fig. 5). Rhizome mass would be expected to increase rapidly in the early years of crop establishment and then remain relatively stable thereafter. Differences in rhizome DM accumulation during 1987 and 1988 are likely a result of the establishment phase of perennial peanut.

Total nonstructural carbohydrate accumulation and distribution followed a similar trend in 1988 as compared to 1987. Rhizome TNC declined during the hot, summer months and increased during the fall (Fig. 10), again suggesting that perennial peanut did not rely heavily on underground reserves for spring growth, but did utilize rhizome reserves for periods of rapid above ground growth during the hot, summer months. In the fall, photosynthate partitioning changed with most being directed to underground rhizomes.

Plant water stress affected rhizome TNC concentrations during periods of dry weather resulting in higher rhizome TNC in water-stressed treatments on 19 May, 8 June, and 25 July (Fig. 10). Above-ground DM accumulation was also less in the water-stressed treatments on these dates, thus indicating that photosynthate was being partitioned underground to rhizomes (and probably the root system in general) at the expense of above-ground growth during plant water stress. Rhizome TNC increased and above-ground DM declined as severity of water stress increased (Figs. 10 and 7). On the average, the RF and CS2 treatments caused an 18% increase in TNC on 19 May as compared to the average of the WW and CS1 treatments. On 8 June, average rhizome TNC in the RF and CS2 treatments (349 g kg^{-1}) was 8 and 17% higher than in the CS1 and WW

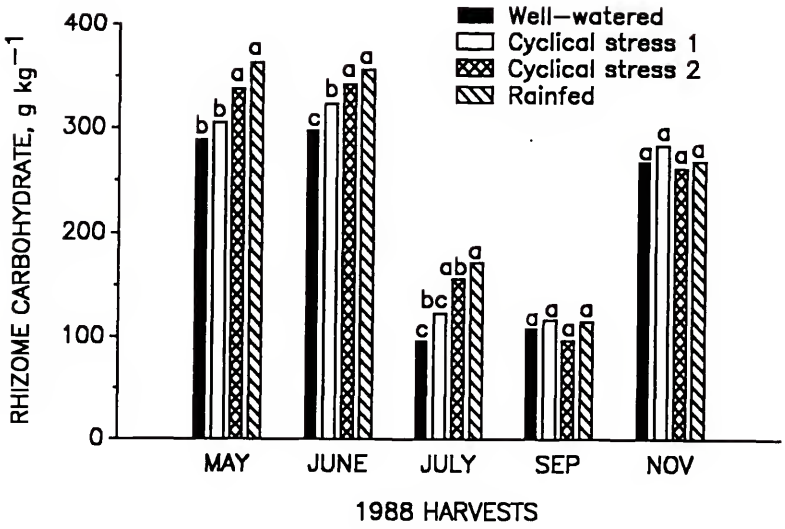

Figure 10. Rhizome nonstructural carbohydrate concentration of perennial peanut as affected by water management treatment on 19 May, 8 June, 25 July, 12 Sep., and 1 Nov. 1988. Different letters above bars within a harvest date indicate differences at $P \leq 0.05$ according to Duncan's New Multiple Range Test.

treatments, respectively. Plant water stress (RF and CS2 treatments) caused rhizome TNC to be 69% higher than in the WW treatment on 25 July. These results are similar to those reported by Hall et al. (1988) who found increased TNC in roots of water stressed alfalfa.

No differences were detected in rhizome TNC during the third and fourth harvest cycles (Fig. 10). Neither was above-ground DM accumulation affected by water management during the remainder of the season. Above average rainfall during August and September precluded the development of plant-water deficits through the remainder of the season.

Total nonstructural carbohydrate concentrations in leaves and stems were fairly constant throughout the season. Leaf TNC was affected only on 19 May, being 39% higher in the RF treatment (118 g kg^{-1}) as compared to the average of the WW, CS1 and CS2 treatments (85 g kg^{-1}). At no other time in 1988 was there a significant effect of water management treatment on leaf or stem TNC. Average seasonal TNC for leaves and stems were 59 and 50 g kg^{-1}, respectively (Data not shown).

In 1988, perennial peanut responded more to water management than in 1987. During 1988 initial growth began earlier (late March) and continued with substantial growth occurring in April. This probably occurred because of somewhat warmer weather in the spring of 1988 as compared to 1987. Average air temperature in April 1988 (20°C) was 2°C warmer than in 1987, and average soil temperature at 100 mm was 4°C higher (24°C in April 1988 as compared to 20°C in 1987). Furthermore, plants in the RF treatment had been exposed to a rather long period of dry weather in October 1987, and initial growth in the spring of 1988

was also under drought conditions. Drying conditions continued throughout the first harvest cycle with the WW treatment receiving relatively frequent irrigations. Soil water deficits also developed during the second harvest cycle in the first part of July. Therefore, plants in the RF and CS2 treatments were subjected to relatively more early season stress in 1988 as compared to 1987. The water deficits in the RF and CS2 treatments were relieved for the remainder of the season after frequent, abundant rainfall occurred in mid summer.

Cumulative above-ground DM for 1988 averaged across water management treatments was calculated in a similar manner to that for 1987, giving a total of 1063 g m^{-2} (Table 9). Average rhizome DM remained practically the same during the 1988 season and actually decreased slightly from 994 g m^{-2} on 12 May to 895 g m^{-2} on 1 November. Even though there was no net gain in rhizome DM, it did accumulate (from its depressed mid summer value) in the fall at the expense of above-ground growth. Summing above-ground and net rhizome DM for the season resulted in a total DM accumulation of 964 g m^{-2}. Again, assuming a 184-day growing season from May through October, 5.2 g m^{-2} d^{-1} was accumulated on the average. Summing forage DM from each of the harvest cycles gives an average cumulative forage yield of 1008 g m^{-2}. Average forage yield was higher in 1988 as compared to 1987 with the yield in each respective harvest cycle being higher except for the last harvest cycle of 1988 when negligible forage DM accumulated.

Seasonal DM accumulation and distribution in 1988 is shown for each water management treatment in Table 10. Above-ground DM was reduced in the CS2 and RF treatments as compared to the WW treatment;

Table 9. Above-ground, rhizome, total, and forage dry matter production by perennial peanut averaged across water management treatments in 1988.

Date	Dry Matter			
	Above-ground	Rhizome	Total	Forage
	----------g m^{-2}----------			
8 June	418	-15[†]	403	363
25 July	344[‡]	-294	50	344
12 Sep.	301[‡]	39	340	301
1 Nov.	-	171	171	-
Cumulative total	1063	-99	964	1008

[†] Represents average dry matter accumulation in rhizomes between the 15 May and 11 June sampling dates.

[‡] Represents dry matter accumulated above the 5-cm stubble height (forage).

Table 10. Seasonal dry matter accumulation and distribution as affected by water management treatment in 1988.

Water management treatment	Dry Matter			
	Above-ground	Rhizome	Total	Forage
	----------g m^{-2}----------			
Well-watered	1194 a*	-117 a	1077 a	1167 a
Cyclical-stress 1	1133 ab	9 a	1142 a	1124 a
Cyclical-stress 2	1057 b	-149 a	908 b	967 b
Rainfed	858 c	-137 a	721 c	767 c

* Means within a column followed by the same letter do not differ at $P \leq 0.05$ as determined by Duncan's New Multiple Range test.

however, the CS1 and CS2 treatments were not different. The CS2 and RF water management treatments caused a significant reduction in cumulative total and cumulative forage DM in 1988 as compared to the average of the WW and CS1 treatments. The CS2 and RF treatments produced 18 and 35% less total DM, and 16 and 33% less forage DM, respectively, than the average of the WW and CS1 treatments. These data indicate that perennial peanut did withstand periods of dry weather for up to two weeks in length throughout the season without adversely affecting harvestable yield; however, extended dry periods of three weeks or more without rainfall or irrigation did reduce available forage by up to one-third compared to the well-watered control and CS1 treatment in 1988.

Physiological Measurements

1987 Season

Single leaf carbon exchange rates (*A*) on specific dates during the first harvest cycle (ended 11 June) as affected by water management treatment are shown in Figure 11. Single leaf carbon exchange rates observed for well-watered perennial peanut were similar to those observed by Lopez et al. (1988) for pigeonpea, Nicolodi et al. (1988) for alfalfa, Sinclair and Horie (1989) for rice (*Oryza sativa* L.) and soybean, and Turner et al. (1985) for sunflower. Twenty-five millimeters of rain accumulated between 12 and 16 May and 75 mm of rainfall occurred from 19 to 21 May. Apparently those rainfall events provided sufficient water to prevent plant water deficits in the CS1, SP, and RF treatments during May. Nevertheless, gravimetric soil water content on 31 May was significantly lower in the SP, CS1, and RF treatments as compared to the WW treatment down to a depth of 750 mm in

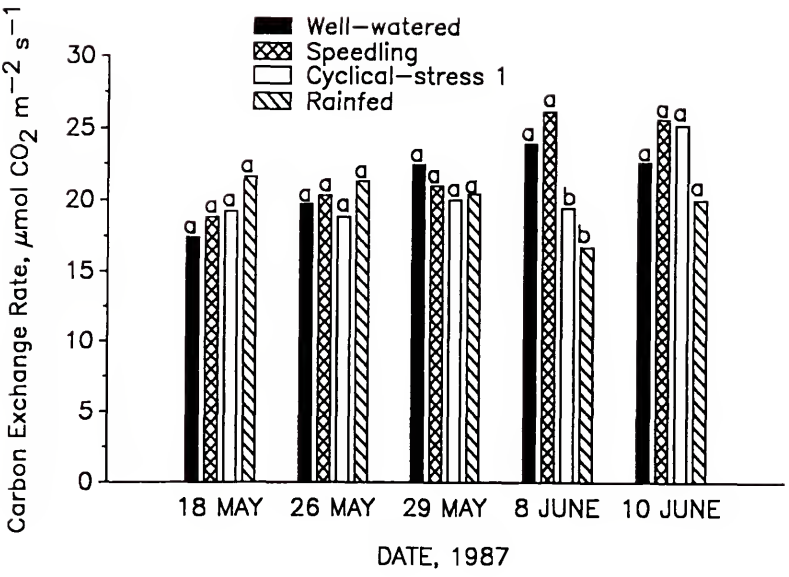

Figure 11. Single leaf carbon exchange rate of perennial peanut as affected by water management treatment on 18, 26, and 29 May, and 8 and 10 June 1987. Different letters above bars within a harvest date indicate differences at $P \leq 0.05$ according to Duncan's New Multiple Range Test.

the soil profile (Fig. 12). On 8 and 10 June, the CS1 treatment was 6 and 8 days, respectively, into a drying cycle and there had been no appreciable rainfall for 17 days (since 21 May). Gravimetric soil water content on 10 June indicated that the WW treatment had a considerably higher soil water content than the other treatments down to a depth of 750 mm (Fig. 13). Below 750 mm there were no statistically significant differences in soil water content. Even after 17 days without rainfall or irrigation, only a 33% reduction in *A* was observed on 8 June in the RF treatment as compared to the WW and SP treatments; however, significant treatment differences in *A* were not apparent on 10 June. There were no irrigation or rainfall events between 8 and 10 June. The lack of a significant response of *A* to drought on 10 June is surprising, since a 33% reduction had been observed two days earlier. Nevertheless, data from both 8 and 10 June suggest that perennial peanut withstood the 19-day drought very well. Presumably, plentiful soil water in the lower depths of the soil profile provided enough water to prevent plant water deficits in the CS1, SP, and RF treatments. The absence of appreciable reductions in *A* after extended dry periods is consistent with the drought resistance exhibited by perennial peanut.

Figure 14 illustrates *A* measured during the third and fourth harvest cycles. Measurements taken near the end of a 2-week dry period in late August failed to reveal any water management treatment effects on *A*. Only at the end of the 41-day dry period during the fourth harvest cycle (29 October) was *A* significantly reduced in the RF treatment as compared to the WW treatment. Even then, *A* was only reduced by 34%. There had been only 10 mm of rainfall (30 September and

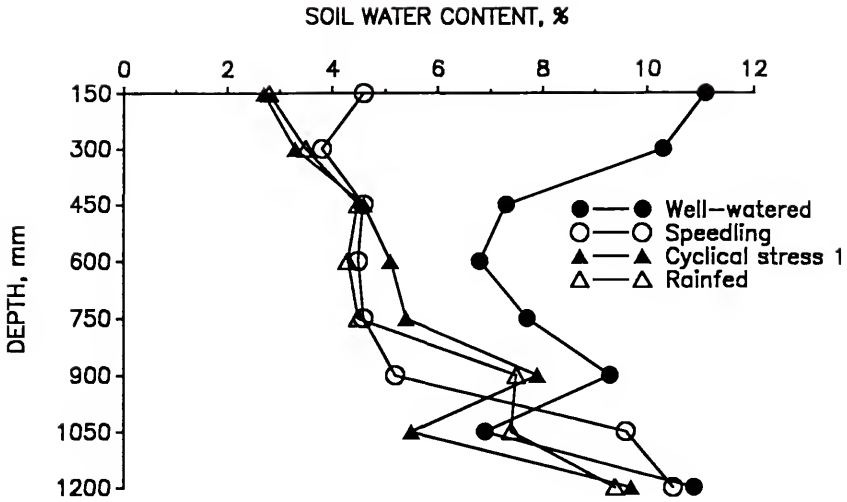

Figure 12. Gravimetric soil water content on 31 May 1987.

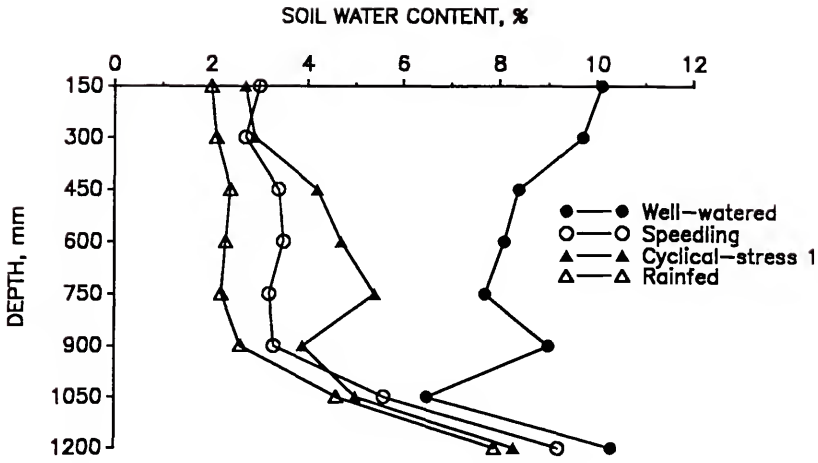

Figure 13. Gravimetric soil water content on 10 June 1987.

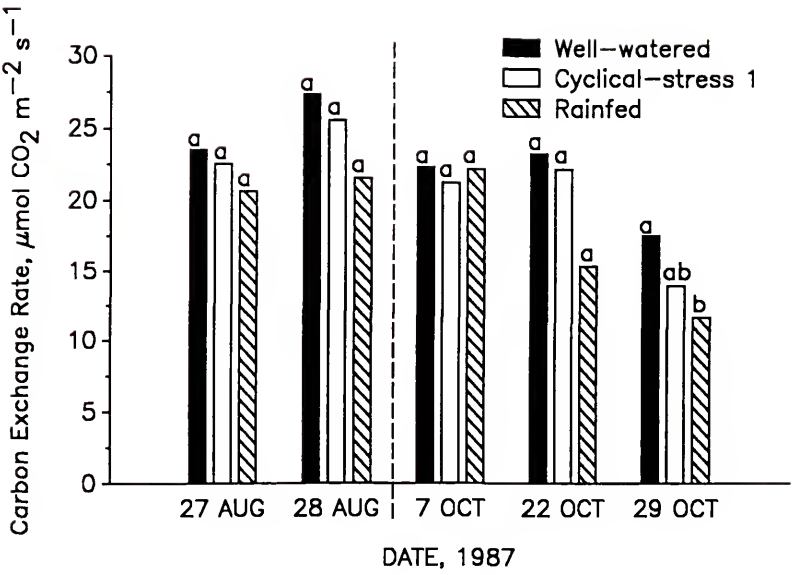

Figure 14. Single leaf carbon exchange rate of perennial peanut as affected by water management treatment on 27 and 28 Aug., and 7, 22 and 29 Oct. 1987. Different letters above bars within a harvest date indicate differences at $P \leq 0.05$ according to Duncan's New Multiple Range Test.

1 October) during the previous 41 days, and gravimetric samples taken at that time (30 October) indicated that soil water contents in the RF and CS1 treatments were lower than in the WW treatment down to a depth of 750 mm (Fig. 15). The RF treatment was also drier than the WW treatment at 900 mm. Below 900 mm, there were no statistically significant differences in soil water content among treatments, but trends for lower soil water content in the CS1 and RF treatments were clearly apparent at 900, 1050 and 1200 mm. Visible signs of drought stress in the RF treatment were apparent at the end of October with opposite leaflets folding together and orienting themselves in such a way as to avoid direct light interception (paraheliotropic leaf movements) during mid-day. This was the only time in 1987 when visible signs of severe plant water stress were observed and gravimetric soil water data indicated that the soil profile was extremely dry in the RF treatment (average of 1.7%) down to the underlying clay layer. Primary differences between soil water on this date and that observed earlier in the season was the greater depletion deep in the soil profile (below 900 mm). Depletion of this water apparently resulted in some plant water deficits and moderate reductions in *A*. From data collected, it appeared that plant water deficits did not develop and *A* remained high as long as plentiful soil water was available deep in the soil profile.

Table 11 shows the numerical data for *A* as illustrated in Figure 11 along with leaf conductance (*g*) and transpiration (*E*), and the ratio *Ci/Ca*. Water management treatment had no effect on *A*, *g*, or *E* during May. Average *A*, *g* and *E* for the three observations (18, 26 and 29 May) were 20.1 μmol CO_2 m^{-2} s^{-1}, 1.6 cm s^{-1} and 0.016 mol m^{-2} s^{-1}, respectively. A

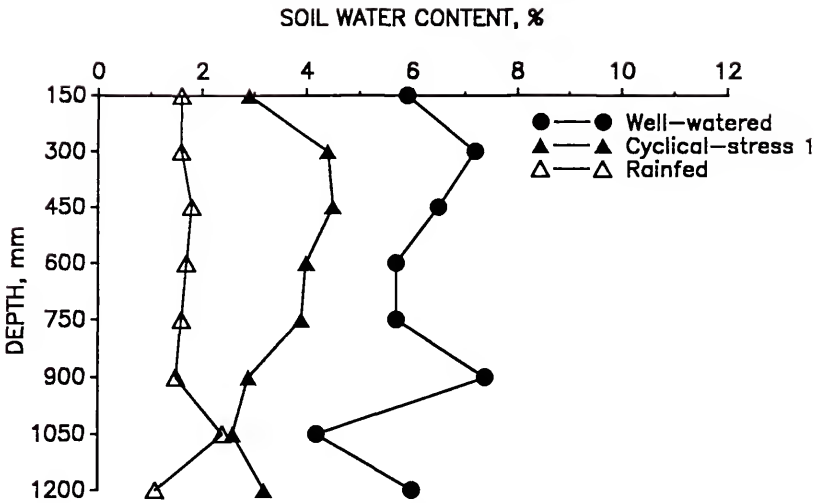

Figure 15. Gravimetric soil water content on 30 Oct. 1987.

Table 11. Single leaf carbon exchange rate (*A*), stomatal conductance (*g*), transpiration (*E*), and the ratio of intercellular to ambient CO_2 concentration (*Ci/Ca*) of perennial peanut as affected by water management treatment on 18, 26 and 29 May, and 8 and 10 June 1987.

Date	Water management treatment	*A*	*g*	*E*	*Ci/Ca*
		μmol CO_2 m^{-2} s^{-1}	cm s^{-1}	mol m^{-2} s^{-1}	
18 May	Well-watered	17.4 a*	1.7 a	0.016 a	0.80 a
	Speedling	18.8 a	1.8 a	0.018 a	0.80 a
	Cyclical-stress 1	19.2 a	1.5 a	0.017 a	0.76 b
	Rainfed	21.6 a	2.1 a	0.020 a	0.80 a
26 May	Well-watered	19.7 a	1.6 a	0.015 a	0.79 a
	Speedling	20.3 a	1.7 a	0.014 a	0.79 a
	Cyclical-stress 1	18.8 a	1.3 a	0.014 a	0.74 a
	Rainfed	21.3 a	1.6 a	0.016 a	0.76 a
29 May	Well-watered	22.4 a	1.7 a	0.016 a	0.76 a
	Speedling	21.0 a	1.5 a	0.014 a	0.74 a
	Cyclical-stress 1	20.0 a	1.3 a	0.012 a	0.71 a
	Rainfed	20.4 a	1.3 a	0.014 a	0.73 a
8 June	Well-watered	23.9 a	1.8 a	0.018 a	0.75 a
	Speedling	26.1 a	2.0 a	0.014 ab	0.76 a
	Cyclical-stress 1	19.4 b	1.2 b	0.014 b	0.72 a
	Rainfed	16.7 b	0.9 b	0.010 b	0.66 a
10 June	Well-watered	22.6 a	1.9 a	0.016 a	0.77 a
	Speedling	25.6 a	2.0 a	0.017 a	0.76 a
	Cyclical-stress 1	25.2 a	2.0 a	0.017 a	0.77 a
	Rainfed	20.0 a	1.1 b	0.014 a	0.68 b

* Means within a column on each date followed by the same letter do not differ at $P \leq 0.05$ as determined by Duncan's New Multiple Range test.

significant reduction in the ratio *Ci/Ca* was detected on 18 May in the CS1 treatment (0.76) as compared to the average of the other three treatments (0.80); however, calculated *Ci* was likely high enough in all treatments (>233 μL L^{-1}) to maximize *A* (at ambient CO_2). Leaf carbon exchange rate has been shown to respond linearly to *Ci* up to 230 μL L^{-1} in various C_3 species (Farquar and Sharkey, 1982). No differences in *Ci/Ca* were detected among water management treatments on 26 or 29 May.

Inconsistent differences in *A*, *g*, *E*, and *Ci/Ca* were detected on 8 and 10 June due to the water stress treatments (CS1 and RF) (Table 11). Single leaf carbon exchange rate, *g* and *E* were 28, 45 and 25% lower, respectively, under water stress (CS1 and RF) compared to the averages of the WW and SP treatments on 8 June. There was a tendency for *Ci/Ca* to be reduced in the RF treatment (0.66) as compared to the WW and SP treatments (0.75). Calculated *Ci* was 203 μL L^{-1} in the RF treatment and 223 μL L^{-1} for the average of the WW and SP treatments. On 10 June, only differences in *g* and *Ci/Ca* were detected, being 44 and 11% lower, respectively, in the RF treatment as compared to the average of the WW, SP and CS1 treatments. Calculated *Ci* values for the RF treatment and the mean of the other three treatments were 208 and 227 μL L^{-1}, respectively. The data taken on 8 and 10 June would indicate that *g* was more sensitive to plant water stress than was *A*. Stomatal conductance was reduced proportionately more than *A* on 8 June, and on 10 June no differences in *A* were detected while *g* was reduced in the RF treatment as compared to the other three treatments. Results obtained by Küppers et al. (1988) for cowpea and Lopez et al. (1988) for pigeonpea have also shown *g* to be more sensitive to plant water stress than *A*. The effect

of *Ci* and data calculated concerning the *Ci/Ca* ratio are somewhat inconclusive. While it appears that calculated *Ci* may have been low enough (203 μL L^{-1}) in the RF treatment on 8 June to have possibly resulted in a reduction in *A*, the *Ci/Ca* ratios were not statistically different among treatments. On 10 June, the *Ci/Ca* ratio was reduced in the RF treatment, but differences in *A* were not detected. Deep rooted characteristics of perennial peanut along with rainfall that occurred may have helped plants in the RF treatment avoid severe water stress during the spring.

Leaf water status did not differ among water management treatments on either 8 or 10 June. There were no significant differences in ψ_L, ψ_π or ψ_P. Mean values for ψ_L, ψ_π and ψ_P were -1.45, -1.75 and 0.30 MPa on 8 June, and -1.14, -1.61 and 0.47 MPa on 10 June, respectively.

Table 12 shows the numerical data for *A* as shown in Figure 14 along with *g*, *E*, and the ratio *Ci/Ca*. Measurements taken on 27 and 28 August during a dry period again revealed no significant effect of water management on *A*, *g*, *E*, and *Ci/Ca* except for *g* on 28 August. As of 28 August, there had not been appreciable rainfall for two weeks since previous precipitation of 120 mm between 11 to 15 August. Stomatal conductance was reduced 19% in the RF treatment as compared to the WW treatment on the 28 August sampling date. Again this would indicate that *g* was more sensitive to plant water deficits than was *A*. Although no differences were detected in *A*, the CS1 treatment caused ψ_L and ψ_π to be reduced on 28 August to -1.51 and -1.70 MPa as compared to -1.17 and -1.45 MPa, respectively, in the WW treatment. Even though reductions in ψ_L and ψ_π were found, they were apparently insufficient to cause

Table 12. Single leaf carbon exchange rate (*A*), stomatal conductance (*g*), transpiration (*E*), and the ratio of intercellular to ambient CO_2 concentration (*Ci/Ca*) of perennial peanut as affected by water management treatment on 27 and 28 August, and 7, 22 and 29 Oct. 1987.

Date	Water management treatment	*A*	*g*	*E*	*Ci/Ca*
		μmol CO_2 m^{-2} s^{-1}	cm s^{-1}	mol m^{-2} s^{-1}	
27 Aug.	Well-watered	23.5 a*	2.8 a	0.024 a	0.82 a
	Cyclical-stress 1	22.5 a	2.2 a	0.021 a	0.80 a
	Rainfed	20.6 a	1.9 a	0.019 a	0.79 a
28 Aug.	Well-watered	27.3 a	2.7 a	0.020 a	0.81 a
	Cyclical-stress 1	25.5 a	2.4 ab	0.019 a	0.80 a
	Rainfed	21.5 a	2.2 b	0.018 a	0.81 a
7 Oct.	Well-watered	22.3 a	1.7 a	0.019 a	0.77 a
	Cyclical-stress 1	21.2 a	1.5 a	0.016 a	0.75 a
	Rainfed	22.1 a	1.4 a	0.016 a	0.73 a
22 Oct.	Well-watered	23.2 a	4.1 a	0.020 a	0.88 a
	Cyclical-stress 1	22.1 a	3.9 a	0.018 a	0.89 a
	Rainfed	15.3 a	2.7 a	0.019 a	0.89 a
29 Oct.	Well-watered	17.5 a	1.0 a	0.010 a	0.72 a
	Cyclical-stress 1	13.9 ab	0.7 ab	0.008 ab	0.71 a
	Rainfed	11.6 b	0.5 b	0.006 b	0.65 b

* Means within a column on each date followed by the same letter do not differ at $P \leq 0.05$ as determined by Duncan's New Multiple Range test.

perturbances in *A*. Unfortunately, no data with respect to ψ_L were taken in the RF treatment on 28 August.

Another series of measurements was taken during a relatively long dry period of 41 days in October. No significant differences were detected in *A*, *g*, *E*, or *Ci/Ca* on 7 or 22 October (Table 12). Average *A*, *g*, *E*, and *Ci/Ca* were 21.9 μmol CO_2 m^{-2} s^{-1}, 1.56 cm s^{-1}, 0.017 mol m^{-2} s^{-1}, and 0.75, respectively, on 7 October; and 20.2 μmol CO_2 m^{-2} s^{-1}, 3.60 cm s^{-1}, 0.019 mol m^{-2} s^{-1}, and 0.89, respectively, on 22 October. On 29 October, water stress (RF treatment) significantly reduced *A*, *g*, *E*, and *Ci/Ca* by 34, 53, 44, and 10%, respectively, as compared to the WW treatment. Calculated *Ci* was 218 and 238 μL L^{-1} in the RF and WW treatments, respectively. Again the data show that *g* was reduced proportionately more than *A* in perennial peanut subjected to soil water deficits. Even though *Ci/Ca* was reduced in the RF treatment as compared to the WW and CS1 treatments, it appears that calculated *Ci* (218 μL L^{-1}) in the RF treatment was likely not low enough to cause *A* to be reduced by one-third as compared to the WW treatment. To address this question, *A* for the WW treatment on 29 October was calculated utilizing the value for stomatal conductance to CO_2 (g_c) from the RF treatment according to the method of Nicolodi et al. (1988). Calculated *A* for the WW treatment based on g_c from the RF treatment was 13.6 μmol CO_2 m^{-2} s^{-1} when in fact actual *A* was 11.6 μmol CO_2 m^{-2} s^{-1} in the RF treatment. Therefore, the reduction in *A* (ie., 17.5 - 13.6 = 3.9) as a result of restricted gas diffusion was 66% of the measured reduction (difference between WW and RF treatment, ie., 17.5 - 11.6 = 5.9). The additional 34% reduction in observed *A* under water stress was presumably due to nonstomatal

(biochemical) mechanisms. Similar results were published by Nicolodi et al. (1988) for water stressed alfalfa.

Total leaf water potential and ψ_P also differed among water management treatments on 29 October being reduced to -3.0 and 0.0 MPa, respectively, in the RF treatment as compared to -1.1 and 0.9 MPa on the average in the WW and CS1 treatments. It is noteworthy that leaves with a ψ_L of -3.0 MPa maintained *A* which was 66% of that in the WW treatment. These results suggest that perennial peanut leaves continue to function even at quite severe water deficits.

Single leaf carbon exchange rate was never reduced by more than one-third during the 1987 growing season, even when subjected to severe soil water deficits during late October. Neither did the *Ci/Ca* ratio ever decrease greatly nor were the decreases in calculated *Ci* drastic under plant water stress. These data relating the physiological response of perennial peanut to water stress are consistent with the minimal effects of plant water stress on photosynthate accumulation and distribution as discussed in the previous sections.

1988 Season

Figure 16 depicts the effect of water management treatment on *A* for five dates during the first harvest cycle (ended 8 June) and on 8 July during the second harvest cycle in 1988. Water management reduced *A* during the dry spring period in 1988. Approximately halfway through the first harvest cycle on 12 May, a reduction of *A* was evident in the RF treatment as compared to the WW, CS1, and CS2 treatments. On 12 May, the RF treatment had received only 28 mm of rainfall in the last 30 days. As a result of this extended dry period *A* was reduced by

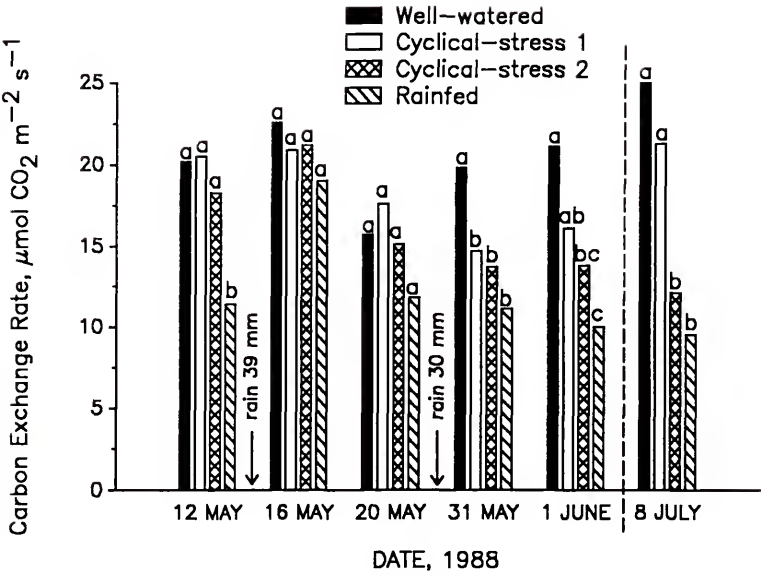

Figure 16. Single leaf carbon exchange rate of perennial peanut as affected by water management treatment on 12, 16, 20 and 31 May, 1 June and 8 July 1988. Different letters above bars within a harvest date indicate differences at $P \leq 0.05$ according to Duncan's New Multiple Range Test.

approximately 40% on 12 May. Thirty-nine millimeters of rainfall on 14 May precluded the further development of water stress and all treatments had similar *A* on both 16 and 20 May. Another 30 mm of rainfall occurred on 25 May; however, reductions in *A* were observed one week later on 31 May and 1 June in all water stress treatments (CS1, CS2, and RF) compared to the WW treatment. The observed reduction of *A* in the water stress treatments after only one week without rainfall was somewhat surprising considering the absence of such responses in 1987. However, absence of pretreatment irrigation, earlier initiation of spring growth, and depletion of soil water by roots deep in the soil profile during the dry spring period probably contributed to the observed responses. Gravimetric soil water content taken on 2 June indicated a reduction in soil water content under all water stress treatments (CS1, CS2 and RF) down to a depth of 1200 mm (Fig. 17). Soil water content in the water stress treatments was reduced at lower depths in the soil profile in 1988 as compared to 1987. Soil water was probably extracted from these depths during extended periods without rainfall (ie. fall 1987 and spring 1988), thereby depleting water reserves that the crop may have had access to in the spring of 1987. Another dry period midway through the second harvest cycle (30 June to 10 July) also caused *A* to be drastically reduced in the CS2 and RF treatments as compared to the WW and CS1 treatments on 8 July (Fig. 16).

Abundant rainfall between 10 July and 3 October precluded the development of plant water stress during that time. Single leaf carbon exchange rate was also unaffected by water management during the fall dry period even though no rainfall occurred after 3 October.

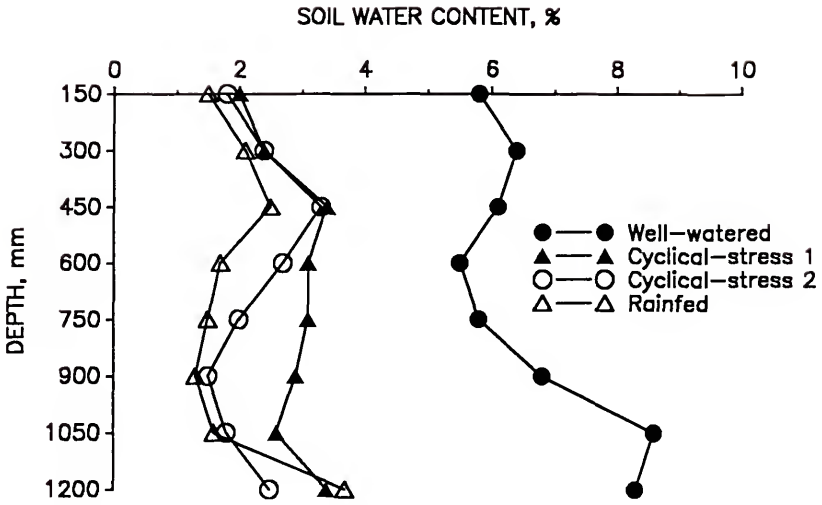

Figure 17. Gravimetric soil water content on 2 June 1988.

Table 13 shows the numerical data for *A* as illustrated in Figure 16 along with *g*, *E*, and *Ci/Ca*. On 12 May, single leaf carbon exchange rate, *g*, *E* and *Ci/Ca* were reduced 42, 67, 55 and 20% in the RF treatment as compared to the average of the WW, CS1 and CS2 treatments. Calculated *Ci* was 191 μL L^{-1} in the RF treatment as compared to 231 μL L^{-1} for the average of the WW, CS1, and CS2 treatments, indicating that relatively low *Ci* may have contributed to the reduction of *A* in plants from the RF treatment. Calculated *A* in the WW treatment based on g_c for the RF treatment was 12.9 μmol CO_2 m^{-2} s^{-1} indicating that 82% of the observed reduction in *A* under water stress (RF treatment) could be accounted for by the stomatal component. There was 39 mm of rainfall on 14 May and even though *A* was not found to be significantly affected by water treatment on 16 May, *g*, *E* and *Ci/Ca* were reduced 36, 19 and 9% under the RF treatment as compared to the average of the WW, CS1, and CS2 treatments. Apparently, the previous plant water deficit prevented complete stomatal opening after soil water was replenished. Calculated *Ci* was 213 μL L^{-1} in the RF treatment as compared to 229 μL L^{-1} for the average of the WW, CS1, and CS2 treatments. On 20 May, no effects of water management treatment on *A*, *g*, *E* or *Ci/Ca* were detected.

Rainfall of 32 mm occurred on 25 May; however, visible symptoms of plant water stress were apparent by 31 May and 1 June. On the average, *A*, *g*, *E* and *Ci/Ca* were reduced by 34, 56, 40 and 14% in the CS1, CS2 and RF treatments as compared to the WW treatment on 31 May. Average calculated *Ci* was 206 μL L^{-1} for the CS1, CS2 and RF treatments and 231 μL L^{-1} in the WW treatment. On 1 June the CS2 and RF treatments caused *A*, *g*, *E* and *Ci/Ca* to be reduced by 41, 74, 62 and 21% as compared to the

Table 13. Single leaf carbon exchange rate (*A*), stomatal conductance (*g*), transpiration (*E*), and the ratio of intercellular to ambient CO_2 concentration (*Ci/Ca*) of perennial peanut as affected by water management treatment on 12, 16, 20 and 31 May, 1 June and 8 July 1988.

Date	Water management treatment	*A*	*g*	*E*	*Ci/Ca*
		μmol CO_2 m^{-2} s^{-1}	cm s^{-1}	mol m^{-2} s^{-1}	
12 May	Well-watered	20.2 a*	1.3 a	0.014 a	0.73 a
	Cyclical-stress 1	20.5 a	1.3 a	0.015 a	0.74 a
	Cyclical-stress 2	18.3 a	1.1 a	0.015 a	0.71 a
	Rainfed	11.4 b	0.4 b	0.007 b	0.58 b
16 May	Well-watered	22.6 a	1.5 a	0.014 a	0.73 a
	Cyclical-stress 1	20.9 a	1.5 a	0.014 a	0.76 a
	Cyclical-stress 2	21.2 a	1.5 a	0.013 a	0.76 a
	Rainfed	19.0 a	1.0 b	0.011 b	0.68 b
20 May	Well-watered	15.7 a	1.0 a	0.013 a	0.70 a
	Cyclical-stress 1	17.6 a	1.0 a	0.013 a	0.68 a
	Cyclical-stress 2	15.1 a	0.8 a	0.012 a	0.69 a
	Rainfed	11.8 a	0.5 a	0.009 a	0.61 a
31 May	Well-watered	19.8 a	1.3 a	0.015 a	0.74 a
	Cyclical-stress 1	14.7 b	0.7 b	0.010 b	0.67 b
	Cyclical-stress 2	13.7 b	0.6 bc	0.010 bc	0.62 b
	Rainfed	11.1 b	0.4 c	0.007 c	0.62 b
1 June	Well-watered	21.1 a	1.8 a	0.019 a	0.76 a
	Cyclical-stress 1	16.1 ab	0.9 ab	0.014 b	0.70 ab
	Cyclical-stress 2	13.7 bc	0.5 b	0.008 bc	0.61 bc
	Rainfed	10.0 c	0.4 b	0.006 c	0.58 c
8 July	Well-watered	25.0 a	1.4 a	0.017 a	0.67 a
	Cyclical-stress 1	21.3 a	1.0 a	0.014 a	0.64 a
	Cyclical-stress 2	12.1 b	0.3 b	0.007 b	0.45 b
	Rainfed	9.5 b	0.3 b	0.006 b	0.44 b

* Means within a column on each date followed by the same letter do not differ at $P \leq 0.05$ as determined by Duncan's New Multiple Range test.

WW treatment. Average calculated *Ci* was 195 μL L^{-1} in the CS2 and RF treatments and 230 μL L^{-1} in the WW treatment.

Again these data indicate that in perennial peanut *g* was reduced to a proportionately greater degree than was *A* under plant water deficits. This in turn would have a direct effect on the observed reduction in *E* as well as causing reduced diffusion of CO_2 through stomata. Since *A* was affected to a lesser extent than *g* by plant water deficits, CO_2 would continue to be assimilated at a relatively rapid rate. However, *Ci* would decline because of restricted gas diffusion into the leaf (stomatal control), thus causing the observed reductions in *Ci/Ca* associated with plant water deficits. Reduced g_c accounted for 73 and 78% of the observed reductions in *A* on 31 May and 1 June, respectively. Therefore, it appears that the biochemical effect of plant water stress on *A* contributed substantially less to the observed reductions than did the stomatal component.

Leaf water potential measurements taken on 1 June indicated that ψ_L and ψ_π were reduced from -1.44 and -1.68 MPa (average of the WW and CS1 treatments), respectively, to -2.28 and -2.06 MPa under water stress (average of the CS2 and RF treatments). Calculated ψ_p was higher in the WW treatment (0.31 MPa) than in the CS2 and RF treatments (0 MPa) with ψ_p in the CS1 treatment (0.16 MPa) not being significantly different from any of the other treatments.

Measurements taken on 8 July following another dry period (30 June to 10 July without significant rainfall) indicated that water stress (CS2 and RF treatments) caused *A*, *g*, *E* and *Ci/Ca* to be reduced 54, 74, 58 and 32% as compared to the average of the WW and CS1 treatments

(Table 13). Average calculated *Ci* was 144 μL L^{-1} in the CS2 and RF treatments and 203 μL L^{-1} on the average in the WW and CS1 treatments. In this case lowered g_c accounted for 94% of the observed reductions in *A* for the plants under water stress (CS2 and RF treatments). As previously mentioned, *g* was reduced more than *A* under water stress.

Leaf water potential measurements were also taken during this dry period. Total leaf water potential in the RF treatment was reduced to -2.15 MPa as compared to -1.44 MPa for the average of the WW, CS1 and CS2 treatments. Calculated ψ_p was not shown to be statistically different but appeared to decline with increasing water stress (0.32, 0.13, 0.05 and 0 MPa in the WW, CS2, CS1 and RF treatments, respectively).

Even though *A* was shown to be reduced by plant water stress on four of the six sampling dates, average *A* in the water-stressed treatments (RF on 12 May; CS1, CS2 and RF on 31 May; and CS2 and RF on 1 June and 8 July) was 12 μmol CO_2 m^{-2} s^{-1}, and still approximately 60% of the rate in the nonstressed treatments (21 μmol CO_2 m^{-2} s^{-1}) (WW, CS1 and CS2 on 12 May; WW on 31 May and 1 June; and WW and CS1 on 8 July). On the average, *g* was only 36% of that in the nonstressed treatments, thus indicating that *g* was more sensitive to plant water stress than *A*. The observed reduction in *Ci/Ca* in the water stress treatments also supports the more sensitive response of stomata since CO_2 diffusion into the leaf is principally controlled by stomata. The *Ci/Ca* ratio and calculated *Ci* were consistently reduced in the water stress treatments, and lowered g_c accounted for 66 to 94% of the observed reductions in *A*. Even though leaf water status indicated severe plant water deficits, at no time

during the season did *A* approach zero. In contrast to many field crops such as corn, soybean, and annual peanut, it appeared that perennial peanut maintained reasonable rates of *A* even though plant water status was considerably reduced.

Plant water deficits did not develop during the remainder of the season because of plentiful rainfall from 10 July to 3 October. Measurements taken on 17 and 24 October revealed no differences in *A*, *g*, *E* or *Ci/Ca* except on 24 October when a difference in *A* was detected (Table 14). Single leaf carbon exchange was reduced 18% in the RF treatment as compared to the CS2 treatment, and *A* in the WW treatment did not differ from either. No data were collected from the CS1 treatment because of a recent irrigation (18 October). Even though gravimetric data taken on 2 November indicated that there were differences in soil moisture content at the 150, 300, 450, 600, 750 and 1050 mm depths (Fig. 18), the cooler than average night temperatures during October may have been limiting growth more than drought.

Single Leaf Carbon Exchange Rate and Specific Leaf N Content

Even though an attempt was made to obtain perennial peanut leaflets with a wide range of specific leaf N (SLN) content, all samples fell within a relatively narrow range from 1.2 to 2.2 g N m^{-2} (Fig. 19). Two of the data points for Florigraze that had high SLN content but relatively low *A* were excluded from the regression analysis. Therefore, 16 data points for Florigraze and 26 for Arbrook were used to compute linear regression equations in an attempt to characterize the relationship between SLN content and *A* (Fig. 19). Since the response

Table 14. Single leaf carbon exchange rate (*A*), stomatal conductance (*g*), transpiration (*E*), and the ratio of intercellular to ambient CO_2 concentration (*Ci/Ca*) of perennial peanut as affected by water management treatment on 17 and 24 Oct. 1988.

Date	Water management treatment	*A*	*g*	*E*	*Ci/Ca*
		μmol CO_2 m^{-2} s^{-1}	cm s^{-1}	mol m^{-2} s^{-1}	
17 Oct.	Well-watered	22.8 a*	1.1 a	0.012 a	0.67 a
	Cyclical-stress 1	21.5 a	1.0 a	0.012 a	0.67 a
	Cyclical-stress 2	19.6 a	0.9 a	0.012 a	0.65 a
	Rainfed	22.9 a	1.1 a	0.010 b	0.66 a
24 Oct.	Well-watered	21.7 ab	1.1 a	0.011 a	0.68 a
	Cyclical-stress 1	-	-	-	-
	Cyclical-stress 2	24.4 a	1.1 a	0.011 a	0.65 a
	Rainfed	20.0 b	1.0 a	0.011 a	0.67 a

* Means within a column on each date followed by the same letter do not differ at $P \leq 0.05$ as determined by Duncan's New Multiple Range test.

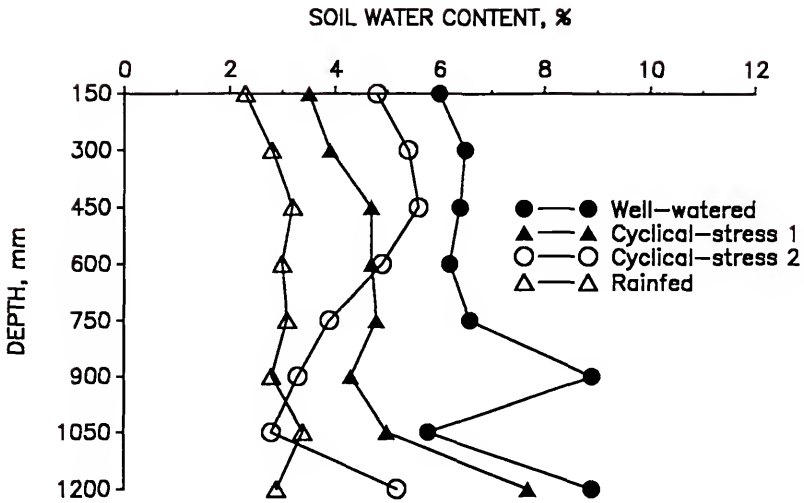

Figure 18. Gravimetric soil water content on 2 Nov. 1988.

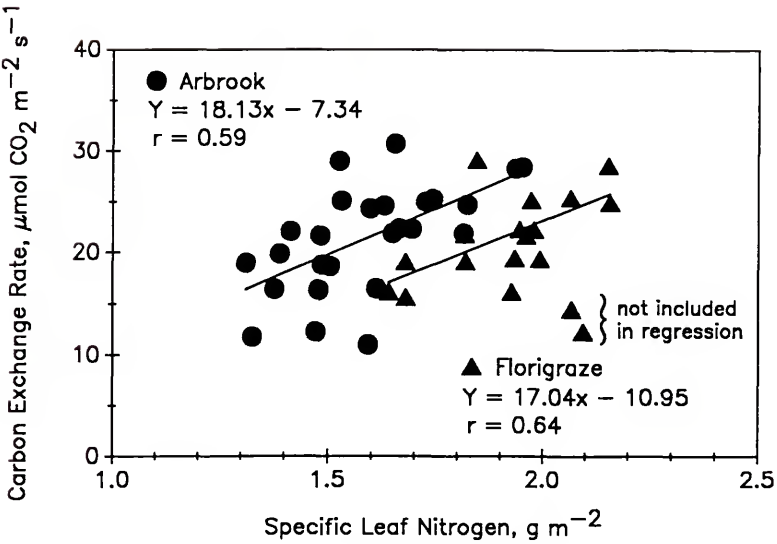

Figure 19. Correlation between specific leaf nitrogen content and single leaf carbon exchange rate of perennial peanut.

function for each cultivar was slightly different, a regression line was computed independently for Florigraze and Arbrook.

The correlation between SLN content and *A* was 0.64 and 0.59 for Florigraze and Arbrook, respectively (Fig. 19). The same general trend is evident for both cultivars showing a positive relationship between SLN and *A*. This would be expected since increasing amounts of N would be used by the plant for additional proteins and enzymes such as light harvesting complex protein and the carboxylating enzyme, rubisco. In general, Florigraze tended to have higher SLN content than Arbrook, and exhibited lower *A* at a given SLN content as compared to Arbrook. However, the range observed in *A* was similar for the two species.

Plant Nitrogen Concentration and *in vitro* Digestibility

1987 Season

Plant N concentration was unaffected by water management treatment on any harvest date; therefore, only means (averaged across water management treatments) are presented in Table 15. Plant N concentration in the forage sample and above-ground plant components was relatively high throughout the season with average concentration being 24, 27, and 15 g kg^{-1} in the forage, leaves, and stems, respectively. These values represent a relatively high level of N with respect to nutritive value of forages and are similar to results reported by Romero et al. (1987) for perennial peanut.

Plant fraction had a significant effect on N concentration on all harvest dates (Table 15). Nitrogen concentration was always higher in the above-ground plant components than it was in rhizomes. On the

Table 15. Nitrogen concentration of perennial peanut forage, and leaf, stem and rhizome plant components (averaged across water management treatments) in 1987.

Plant fraction	Date					
	15 May	1 June	11 June	23 July	8 Sep.	2 Nov.
	----------g kg^{-1}----------					
Forage	-	24.2 bA*	25.2 aA	24.3 bA	23.8 aA	24.6 bA
Leaf	28.5 aA	26.6 aAB	26.9 aA	27.4 aA	23.9 aB	28.7 aA
Stem	17.8 bA	15.4 cBC	13.7 bCD	15.9 cB	12.9 bD	13.8 cCD
Rhizome	11.9 cB	11.5 dB	13.5 bA	10.9 dB	9.9 cC	11.5 cB

* Means within a column followed by the same lowercase letter and means within a row followed by the same uppercase letter do not differ at $P \leq 0.05$ as determined by Duncan's New Multiple Range Test.

average, stem and rhizome components contained 45 and 57% less N, respectively, than the leaf component.

Mean IVOMD values, averaged across water management treatments, for each harvest are presented in Table 16. Even though statistical differences are noted across harvest dates, IVOMD was relatively high in the forage sample as well as leaf and stem components throughout the season, and there was no mid-summer decline as is often seen in other forages (Jolliff et al., 1979; Sleper and Mott, 1976). Plant fraction affected IVOMD throughout the season (except for the first harvest of relatively immature plants in mid May) with IVOMD of the stem averaging 14% less than that in the leaf.

In vitro organic matter digestibility was slightly affected during the season by water management. Stems of plants from the RF treatment subjected to the prolonged dry period (41 days) in the fall were higher in digestibility (587 g kg^{-1}) than those in the CS1 and WW treatments (553 g kg^{-1}). However, forage that accumulated during the fall (last harvest cycle) was negligible, and any decline in IVOMD of the plants at that time would be of little consequence in terms of animal nutrition and forage utilization.

1988 Season

In general, plant N concentration in the forage sample as well as the leaf and stem components was relatively high throughout the 1988 growing season (Table 17) as had been the case in 1987. Average N concentrations for the season were 30, 31, and 18 g kg^{-1} in the forage, leaves, and stems, respectively, being slightly higher than those reported in 1987.

Table 16. *In vitro* organic matter digestibility of perennial peanut forage, and leaf and stem components (averaged across water management treatments) in 1987.

Plant fraction	Date					
	15 May	1 June	11 June	23 July	8 Sep.	2 Nov.
	----------g kg^{-1}----------					
Forage	-	730 aC*	735 aBC	742 aAB	736 aBC	747 aA
Leaf	771 aA	725 aE	728 aDE	742 aC	733 aD	763 bB
Stem	725 aA	657 bB	641 bB	638 bB	608 bC	565 cD

* Means within a column followed by the same lowercase letter and means within a row followed by the same uppercase letter do not differ at $P \leq 0.05$ as determined by Duncan's New Multiple Range Test.

Table 17. Nitrogen concentration of perennial peanut forage, and leaf, stem and rhizome plant components (averaged across water management treatments) in 1988.

Plant fraction	Date					
	19 May	2 June	8 June	25 July	12 Sep.	1 Nov.
	----------g kg^{-1}----------					
Forage	-	-	25.6 bC	32.6 bA	31.3 bB	-
Leaf	27.7 aD	28.3 aCD	29.2 aC	34.7 aA	34.8 aA	32.5 aB
Stem	17.1 bC	16.8 bC	16.8 cC	20.4 cA	19.1 cB	15.2 bD
Rhizome	11.5 cD	12.6 cC	12.9 dBC	14.2 dA	13.3 dB	11.5 cD

* Means within a column followed by the same lowercase letter and means within a row followed by the same uppercase letter do not differ at $P \leq 0.05$ as determined by Duncan's New Multiple Range Test.

Plant fraction had a consistent effect on N concentration throughout the season (Table 17). Again, the above-ground plant components contained more N than the rhizomes and, on the average, N concentration in the stems and rhizomes was 44 and 59% lower, respectively, than that in the leaves.

Water management treatment did have a slight effect on plant N concentration on two occasions in 1988. An effect of water management was observed at the 2 June harvest with leaf N concentration being reduced from 29.8 g kg^{-1} on the average in the WW and CS1 treatments to 26.8 g kg^{-1} on the average in the CS2 and RF treatments, respectively. However, those differences had disappeared by 8 June at the end of the first harvest cycle. Furthermore, such small effects do not represent differences which would appreciably affect the nutritive value of the crop. Water management treatment also had an effect on plant N concentration in the leaf and stem components as well as the composite forage sample taken at the end of the second harvest cycle on 25 July (Table 18). Water stress (CS2 and RF treatments) led to relatively higher forage and leaf N concentrations as compared to the WW and CS1 treatments, but only the RF treatment caused stem N to increase as compared to the other three treatments. Nitrogen concentration in the forage sample increased in the RF and CS2 treatments as compared to the WW treatment. Donovan and Meek (1983) have also reported higher protein concentrations under dry as compared to well-irrigated conditions in alfalfa. Even though the differences in N concentration are significant, perennial peanut had relatively high concentrations of N

Table 18. Nitrogen concentration of perennial peanut forage, and leaf and stem components as affected by water management treatment on 25 July 1988.

Water management treatment	Forage	Plant Component	
		Leaf	Stem
	----------g kg^{-1}----------		
Well-watered	29.6 c*	32.8 b	19.1 b
Cyclical-stress 1	31.6 bc	32.9 b	19.6 b
Cyclical-stress 2	32.7 b	35.9 a	19.7 b
Rainfed	36.3 a	37.0 a	22.9 a

* Means within a column followed by the same letter do not differ at $P \leq 0.05$ as determined by Duncan's New Multiple Range Test.

under all water management treatments throughout the entire growing season.

Mean IVOMD, averaged across water management treatments, for each harvest is presented in Table 19. As in 1987, IVOMD was relatively high in the forage samples as well as the leaf and stem components throughout the season except for quite low values in the stem component on 1 November. As previously mentioned, forage accumulated during the fall was negligible and low stem digestibility at that time of year would likely be of no consequence for forage utilization. Plant component had a consistent effect on IVOMD throughout the season with stem IVOMD being 16% less than leaf IVOMD on the average.

Water management treatment impacted plant IVOMD on two occasions during the 1988 growing season. Stem IVOMD was increased by 8.5% at the end of the first harvest cycle (ended 8 June) in the RF treatment (661 g kg^{-1}) as compared to the average of the WW, CS1 and CS2 treatments (609 g kg^{-1}). Water stress (CS2 and RF treatments) also caused an increase in IVOMD during the second harvest cycle (ended 25 July) in the leaf and stem fractions as well as the forage sample (Table 20). Even though differences occurred, the leaf component and forage IVOMD was relatively high under all water management treatments. Stem digestibility was reduced to an average of 589 g kg^{-1} in the WW and CS1 treatments; however, samples taken represent the whole stem to ground level which includes unpalatable material that would probably never be utilized by the grazing animal or harvested by mechanical equipment. No other effects of water management treatment were detected on IVOMD during the season.

Table 19. *In vitro* organic matter digestibility of perennial peanut forage, and leaf and stem components (averaged across water management treatments) in 1988.

Plant fraction	Date					
	19 May	2 June	8 June	25 July	12 Sep.	1 Nov.
	----------g kg^{-1}----------					
Forage	-	-	695 bA*	700 bA	690 bA	-
Leaf	728 aAB	713 aC	716 aC	721 aBC	701 aD	731 aA
Stem	676 bA	639 bB	622 cC	609 cD	602 cD	487 bE

* Means within a column followed by the same lowercase letter and means within a row followed by the same uppercase letter do not differ at $P \leq 0.05$ as determined by Duncan's New Multiple Range Test.

Table 20. *In vitro* organic matter digestibility of perennial peanut forage, and leaf and stem components as affected by water management treatment on 25 July 1988.

Water management treatment	Forage	Plant Component	
		Leaf	Stem
	----------g kg^{-1}----------		
Well-watered	683 c*	711 b	579 c
Cyclical-stress 1	689 bc	713 b	599 bc
Cyclical-stress 2	699 b	728 a	615 ab
Rainfed	728 a	730 a	639 a

* Means within a column followed by the same letter do not differ at $P \leq 0.05$ as determined by Duncan's New Multiple Range Test.

Forage IVOMD and N concentration were relatively high under the various water management treatments throughout both seasons. No decline in digestibility or N concentration was noted during the hot summer months, and perennial peanut would be considered a forage crop of high nutritive value. Romero et al. (1987) in a study comparing alfalfa and perennial peanut also concluded that perennial peanut is of high nutritive value and equal to alfalfa for ruminant animal nutrition.

SUMMARY AND CONCLUSIONS

A field-grown perennial peanut crop, established under well-irrigated conditions in 1986, was subjected in 1987 and 1988 to several water management treatments designed to create varying degrees of plant water deficits. Four water management treatments were imposed on perennial peanut in both 1987 and 1988. In 1987, the treatments were as follows: 1) well-watered (WW), irrigated every 2 to 4 days during periods of dry weather throughout the growing season; 2) cyclical stress (CS1), received complete soil water recharge at 10 to 14 day intervals during dry weather; 3) water withheld until stomata began to close, then light frequent irrigation to replenish daily evapotranspiration (SP); and 4) rainfed (RF). The SP treatment was suspended after the first harvest cycle in 1987 (ended 11 June), and thereafter received the same irrigation as the CS1 treatment during the rest of the season. In 1988, the treatments were as follows: 1) well-watered (WW), received irrigation every 2 to 4 days during periods without significant rainfall; 2) 2-week cyclical stress (CS1), received irrigation to achieve complete soil water recharge every 14 days during periods without rainfall; 3) 3-week cyclical stress (CS2), received irrigation to achieve complete soil water recharge every 21 days during periods without rainfall; and 4) rainfed (RF). Water management treatments were the same in both years except for treatment no. 3. Since the SP treatment produced similar results as the WW and CS1 treatments in 1987,

it was replaced with the CS2 treatment in 1988. Dry matter accumulation and distribution, rhizome TNC concentration, *A*, *g*, leaf water status, and nutritive value were determined to quantify the response of the crop to drying soil conditions.

Rainfall was below the 30-year mean during the spring in both 1987 and 1988. Typical abundant summer rainfall occurred in both years and the fall was quite dry, especially in 1987. In general, rainfall patterns were typical of those observed in north Florida, and the drier than normal spring weather probably tended to amplify the responses to irrigation during those periods compared to what might be expected with more normal rainfall amounts.

Gravimetric soil water data indicated that the water management regimes imposed were effective in creating real differences in available soil water at various times throughout the study. Water management treatment affected DM distribution and accumulation of perennial peanut only during periods of severe soil water deficits (fall 1987, spring and summer 1988). Increasing severity of plant water stress caused a decrease in above-ground growth and an increase in rhizome TNC, indicating that photosynthate was being partitioned underground at the expense of above-ground growth during periods of plant water deficits. Total above-ground DM in the RF treatment was reduced 18 and 26% in 1987 and 1988, respectively, as compared to the average of the WW and CS1 treatments. Above-ground DM was also reduced 11% in the CS2 treatment in 1988 as compared to the WW treatment. Seasonal forage DM (DM above 5-cm cutting height) accumulation was unaffected by water treatment in 1987; however, an extremely dry spring followed by a summer dry period

(30 June to 10 July) caused seasonal forage DM production to be reduced by up to one-third in the water stress treatments (CS2 and RF) as compared to the well-watered control and CS1 treatments in 1988. In 1987, there was more soil water deep in the profile for the water stress treatments than occurred in 1988. A dry spring, earlier initiation of plant growth, and more fully established plants all probably contributed to depletion of soil water deep in the profile in 1988. Depletion of this soil water reserve during the spring and early summer of 1988 contributed to the greater response of plants to irrigation than was observed in 1987.

Rhizomes constituted approximately two-thirds of the total DM present at the end of any given harvest cycle, except the fall (last) harvest cycle when they constituted approximately 85% of the total DM present. Rhizome DM present in the fall of 1987 was substantially higher than in the spring; however, in 1988 there was relatively little net change in rhizome DM from spring to fall. In both years, rhizome DM was depleted as rapid above-ground growth occurred in early- and mid-summer (June-July), but accumulated rapidly at the expense of above-ground growth in the fall (September-November).

Single leaf carbon exchange rate and the other physiological measurements indicated that perennial peanut was relatively unresponsive to water management until severe soil water deficits occurred (fall 1987, spring and summer 1988). Even under extremely dry conditions when *A* was significantly reduced by plant water stress (RF, or CS2 and RF treatments), average *A* was found to be 66% of the WW rate in 1987 and 57% of the rate for nonstressed plants in 1988. Stomatal conductance

was affected to a substantially greater degree than *A*, being reduced 61% on the average by water stress as compared to an average reduction of 39% in *A*. There were also two occasions when a significant reduction in *g* was detected, yet *A* was unaffected (10 June 1987 and 16 May 1988).

A reduction in the *Ci/Ca* ratio often coincided with reduced *A* suggesting that stomatal control over gas diffusion may have been limiting CO_2 supply to the leaf thus causing a reduction in *A* due to limited substrate. Calculated *Ci* was below 200 $\mu L\ L^{-1}$ on several occasions and was as low as 144 $\mu L\ L^{-1}$ on one occasion (8 July 1988) which is certainly low enough to limit *A* in C_3 plants. The stomatal mechanism (restricted gas diffusion) consistently accounted for two-thirds or more of the observed reductions in *A* under water stress. However, it is likely that both nonstomatal (biochemical) as well as stomatal mechanisms were limiting *A* in perennial peanut subjected to plant water deficits.

Single leaf carbon exchange rate for Florigraze and Arbrook perennial peanut cultivars correlated positively to SLN content. This would be expected since increasing amounts of N would be used by the plant for additional proteins and enzymes such as light harvesting complex protein and the carboxylating enzyme, rubisco. In general, Florigraze tended to have higher SLN content than Arbrook, and exhibited lower *A* at a given SLN content as compared to Arbrook. However, the range observed in *A* was similar for the two cultivars.

Plant component affected N concentration and IVOMD throughout both seasons. On the average, N concentration and IVOMD were 44 and 15% lower, respectively, in the stems as compared to the leaves. However,

forage IVOMD and N concentration were relatively high under the various water management treatments throughout both seasons. No decline in digestibility or N concentration was noted during the hot summer months, and perennial peanut would be considered a forage crop of high nutritive value.

Deep rooted characteristics of perennial peanut resulted in plant productivity which was insensitive to water management during relatively short periods of dry weather (2 to 3 weeks) unless soil moisture reserves deep in the profile had been depleted (summer 1988). It appeared that perennial peanut was capable of using soil water deep in the profile to avoid tissue water deficits. In addition, even when soil water was severely depleted and leaf water potential declined as low as -3.0 MPa in the RF treatment, stomata did not close completely and some carbon assimilation continued. Results of this study suggested that irrigation of perennial peanut would increase forage production only during periods of severe soil water deficits. During dry periods, replenishment of the soil profile with water at 2-week intervals resulted in similar forage yields to those from treatments irrigated more frequently.

APPENDIX

Table A-1. Rainfall and irrigation during the establishment season (April through October, 1986) of Florigraze perennial peanut grown at Gainesville, Florida.

Date	Rainfall	Irrigation	Date	Rainfall	Irrigation
	---mm---			---mm---	
13 Apr.	10	-	11 July	8	-
18	-	13	13	8	19
21	6	-	21	6	8
28	-	13	22	5	-
			23	3	
1 May	-	13	24	16	-
5	-	13	26	3	-
8	-	13	27	25	-
16	-	15	28	6	-
18	-	8			
19	5	-	2 Aug.	2	-
20	20	-	3	10	-
21	1	-	4	4	-
25	-	13	5	3	-
30	-	13	6	1	-
			7	21	-
1 June	5	-	11	13	-
2	10	-	12	17	-
8	-	20	13	11	-
10	24	-	14	27	-
11	2	-	15	2	-
13	9	-	17	1	-
14	44	-	19	1	-
15	8	-	20	51	-
16	1	-	21	13	-
18	10	-	22	4	-
19	23	-	24	5	-
20	3	-	25	2	
21	1	-	27	1	-
30	4	-	28	2	-
			29	21	
1 July	5	-	31	4	-
3	10	-			
5	8		1 Sep.	1	-
7	36	-	3	1	-

Table A1. continued.

Date	Rainfall	Irrigation
	---------mm----------	
5 Sep.	30	-
6	1	-
9	21	-
10	9	-
11	5	-
13	6	-
18	3	-
26	-	18
28	4	-
3 Oct.	-	19
7	10	-
8	6	-
9	16	-
10	36	-
25	2	-
26	1	-
27	13	-
29	6	-
30	8	-

Table A-2. Establishment season forage dry matter production of Florigraze perennial peanut harvested on 31 Oct. 1986.

Sample Site	Forage Dry Matter
	----------g m^{-2}----------
1	279
2	320
3	293
4	277
5	239
6	249
mean	276

Table A-3. Rainfall and irrigation for the four water management treatments imposed on Florigraze perennial peanut grown at Gainesville, Florida, in 1987.

Date	Rainfall	Irrigation			
		Well-watered	Speedling	Cyclical stress 1	Rainfed
	---mm---				
3 Apr.	5	-	-	-	-
4	1	-	-	-	-
9	-	14	14	14	14
15	6	-	-	-	-
16	-	8	8	8	8
18	-	6	6	6	6
19	-	6	6	6	6
21	-	8	8	8	8
22	-	13	13	13	13
24	-	38	38	38	38
27	-	28	-	-	-
29	-	19	-	-	-
1 May	-	19	7	-	-
2	-	-	8	-	-
3	-	19	6	44	-
4	-	-	5	-	-
5	-	19	4	-	-
6	-	-	4	-	-
7	-	19	4	-	-
8	-	-	3	-	-
9	1	19	4	-	-
11	-	19	-	-	-
12	4	-	-	45	-
13	6	-	-	-	-
14	7	-	-	-	-
16	8	-	-	-	-
17	-	19	-	-	-
19	39	-	-	-	-
20	11	-	-	-	-
21	25	-	-	-	-
22	2	-	-	-	-
25	-	19	-	-	-
27	5	19	5	-	-
29	-	19	7	-	-
31	-	15	7	-	-
2 June	-	18	8	38	-
4	-	19	4	-	-
6	2	19	5	-	-

Table A-3. continued.

Date	Rainfall	Irrigation			
		Well-watered	Speedling	Cyclical stress 1	Rainfed
	mm				
8 June	-	19	4	-	-
10	-	19	4	-	-
13	-	19	38	38	-
14	5	-	-	-	-
20	-	19	-	-	-
22	14	-	-	-	-
23	7	-	-	-	-
24	1	-	-	-	-
26	6	-	-	-	-
27	35	-	-	-	-
28	1	-	-	-	-
29	5	-	-	-	-
2 July	5	-	-	-	-
3	1	-	-	-	-
6	-	17	-	-	-
7	1	-	-	-	-
8	1	-	-	-	-
9	26	-	-	-	-
10	12	-	-	-	-
14	4	-	-	-	-
15	4	-	-	-	-
18	1	-	-	-	-
19	2	8	-	-	-
20	1	-	-	-	-
21	20	-	-	-	-
24	14	-	-	-	-
25	1	-	-	-	-
26	1	-	-	-	-
28	5	-	-	-	-
29	-	19	-	-	-
31	1	-	-	-	-
3 Aug.	2	-	-	-	-
4	10	-	-	-	-
5	1	-	-	-	-
8	-	19	-	-	-
10	89	-	-	-	-
11	6	-	-	-	-
12	3	-	-	-	-
14	2	-	-	-	-
15	2	-	-	-	-

Table A-3. continued.

Date	Rainfall	Irrigation			
		Well-watered	Speedling	Cyclical stress 1	Rainfed
	mm				
19 Aug.	-	20	-	-	-
22	-	25	-	-	-
26	-	20	-	-	-
29	-	32	32	32	-
30	1	-	-	-	-
2 Sep.	2	-	-	-	-
3	1	-	-	-	-
5	-	25	-	-	-
6	2	-	-	-	-
8	1	-	-	-	-
9	-	13	-	-	-
11	1	-	-	-	-
12	47	-	-	-	-
13	3	-	-	-	-
18	1	-	-	-	-
19	31	-	-	-	-
25	-	18	-	-	-
29	1	-	-	-	-
30	3	-	-	-	-
1 Oct.	7	-	-	-	-
5	-	25	25	25	-
12	-	10	-	-	-
18	-	32	32	32	-

Table A-4. Rainfall and irrigation for the four water management treatments imposed on Florigraze perennial peanut grown at Gainesville, Florida, in 1988.

Date	Rainfall	Irrigation			
		Well-watered	Cyclical stress 1	Cyclical stress 2	Rainfed
	mm				
29 Mar.	-	19	5	19	-
2 Apr.	-	13	25	-	-
7	8	-	-	-	-
8	-	13	-	-	-
11	13	-	-	-	-
12	6	-	-	-	-
13	5	-	-	-	-
19	1	-	-	-	-
20	3	-	-	-	-
22	-	13	25	-	-
27	-	13	-	25	-
1 May	13	-	-	-	-
5	-	19	-	-	-
8	-	19	38	-	-
13	-	15	-	-	-
14	39	-	-	-	-
19	-	18	-	-	-
23	-	20	-	-	-
25	30	-	-	-	-
30	-	19	-	-	-
3 June	-	20	46	-	-
6	10	-	-	-	-
7	16	-	-	-	-
9	1	-	-	-	-
12	-	25	-	38	-
16	-	15	-	-	-
19	-	18	-	-	-
21	10	-	-	-	-
24	-	20	46	-	-
25	6	-	-	-	-
26	10	-	-	-	-
28	12	-	-	-	-
29	18	-	-	-	-
2 July	2	-	-	-	-
8	-	18	-	-	-
11	8	-	-	-	-

Table A-4. continued.

Date	Rainfall	Irrigation			
		Well-watered	Cyclical stress 1	Cyclical stress 2	Rainfed
	mm				
14 July	30	-	-	-	-
15	7	-	-	-	-
20	8	-	-	-	-
21	10	-	-	-	-
23	7	-	-	-	-
24	23	-	-	-	-
25	1	-	-	-	-
27	1	-	-	-	-
30	1	19	-	-	-
31	1	-	-	-	-
1 Aug.	25	-	-	-	-
3	8	-	-	-	-
4	4	-	-	-	-
5	1	-	-	-	-
6	13	-	-	-	-
7	1	-	-	-	-
8	17	-	-	-	-
9	4	-	-	-	-
10	2	-	-	-	-
11	6	-	-	-	-
12	6	-	-	-	-
13	1	-	-	-	-
14	50	-	-	-	-
15	1	-	-	-	-
16	38	-	-	-	-
17	28	-	-	-	-
18	27	-	-	-	-
19	6	-	-	-	-
23	1	-	-	-	-
24	-	15	-	-	-
25	2	-	-	-	-
27	2	-	-	-	-
28	71	-	-	-	-
30	4	-	-	-	-
31	60	-	-	-	-
2 Sep.	-	-	-	-	-
3	1	-	-	-	-
6	168	-	-	-	-
7	38	-	-	-	-

Table A-4. continued.

Date	Rainfall	Irrigation			
		Well-watered	Cyclical stress 1	Cyclical stress 2	Rainfed
	mm				
8 Sep.	2	-	-	-	-
9	34	-	-	-	-
10	1	-	-	-	-
16	2	-	-	-	-
19	1	-	-	-	-
20	7	-	-	-	-
22	12	-	-	-	-
25	-	15	-	-	-
26	1	-	-	-	-
27	11	-	-	-	-
30	5	-	-	-	-
1 Oct.	4	-	-	-	-
2	4	-	-	-	-
3	1	-	-	-	-
4	24	-	-	-	-
11	-	18	-	-	-
18	-	18	36	-	-
22	-	15	-	-	-
25	-	18	-	36	-
29	-	15	-	-	-

Table A-5. Gravimetric soil water content as affected by water treatment in 1987.

Water treatment	Depth, mm							
	150	300	450	600	750	900	1050	1200
	----------% water----------							
	-- 31 May --							
Well-watered	11.1a*	10.3a	7.3a	6.8a	7.7a	9.3a	6.9a	10.9a
Speedling	4.6b	3.8b	4.6b	4.5b	4.6b	5.2a	9.6a	10.5a
Cyclical-stress 1	2.7c	3.3b	4.6b	5.1b	5.4b	7.9a	5.5a	9.7a
Rainfed	2.8c	3.5b	4.5b	4.3b	4.5b	7.5a	7.4a	9.4a
	-- 10 June --							
Well-watered	10.1a	9.7a	8.4a	8.1a	7.7a	9.0a	6.5a	10.3a
Speedling	3.0b	2.7b	3.4bc	3.5bc	3.2c	3.3a	5.6a	9.2a
Cyclical-stress 1	2.7bc	2.9b	4.2b	4.7b	5.4b	3.9a	5.0a	8.3a
Rainfed	2.0c	2.1b	2.4c	2.3c	2.2c	2.6a	4.6a	7.9a
	-- 30 October --							
Well-watered	5.9a	7.2a	6.5a	5.7a	5.7a	7.4a	4.2a	6.0a
Cyclical-stress 1	2.9b	4.4b	4.5b	4.0b	3.9b	2.9ab	2.6a	3.2a
Rainfed	1.6c	1.6c	1.8c	1.7b	1.6b	1.5b	2.4a	1.1a

* Means within a column for each date followed by the same letter do not differ at $P \leq 0.05$ as determined by Duncan's New Multiple Range test.

Table A-6. Gravimetric soil water content as affected by water treatment in 1988.

Water treatment	Depth, mm							
	150	300	450	600	750	900	1050	1200
	% water							
	-- 2 June --							
Well-watered	5.8a*	6.4a	6.1a	5.5a	5.8a	6.8a	8.6a	8.3a
Cyclical-stress 1	2.0b	2.4b	3.4b	3.1b	3.1b	2.9ab	2.6ab	3.4a
Cyclical-stress 2	1.8b	2.4b	3.3b	2.7b	2.0b	1.5b	1.8b	2.5a
Rainfed	1.5b	2.1b	2.5b	1.7b	1.5b	1.3b	1.6b	3.7a
	-- 8 June --							
Well-watered	6.6a	7.2a	6.6a	6.6a	7.4a	8.6a	6.3a	10.6a
Cyclical-stress 1	5.2b	3.6b	3.6c	3.7b	4.4b	3.7a	3.1b	3.5a
Cyclical-stress 2	4.6bc	4.3b	4.8b	4.1b	2.7b	2.0a	1.8b	2.3a
Rainfed	3.6c	1.8c	1.9d	2.1c	2.0b	1.2a	1.6b	1.1a
	-- 2 November --							
Well-watered	6.0a	6.5a	6.4a	6.2a	6.6a	8.9a	5.8a	8.9a
Cyclical-stress 1	3.5c	3.9c	4.7b	4.7b	4.8b	4.3a	5.0ab	7.7a
Cyclical-stress 2	4.8b	5.4b	5.6a	4.9b	3.9bc	3.3a	2.8c	5.2a
Rainfed	2.3d	2.8d	3.2c	3.0c	3.1c	2.8a	3.4bc	2.9a

* Means within a column for each date followed by the same letter do not differ at $P \leq 0.05$ as determined by Duncan's New Multiple Range test.

Table A-7. Rhizome total nonstructural carbohydrate concentration as affected by water treatment in 1987.

Water treatment	Date					
	15 May	1 June	11 June	23 July	8 Sep.	2 Nov.
	----------g kg^{-1}----------					
Well-watered	163 a*	151 a	245 a	94 a	121 b	324 a
Speedling	185 a	185 a	269 a	-	-	-
Cyclical-stress 1	208 a	217 a	285 a	94 a	147 ab	323 a
Rainfed	234 a	186 a	296 a	137 a	167 a	359 a

* Means within a column followed by the same letter do not differ at $P \leq 0.05$ as determined by Duncan's New Multiple Range test.

Table A-8. Rhizome total nonstructural carbohydrate concentration as affected by water treatment in 1988.

Water treatment	Date					
	19 May	2 June	8 June	25 July	12 Sep.	1 Nov.
	----------g kg^{-1}----------					
Well-watered	289 b*	284 b	298 c	97 c	109 a	268 a
Cyclical-stress 1	305 b	298 b	323 b	123 bc	117 a	283 a
Cyclical-stress 2	337 a	332 a	342 a	156 ab	97 a	261 a
Rainfed	363 a	337 a	356 a	172 a	115 a	268 a

* Means within a column followed by the same letter do not differ at $P \leq 0.05$ as determined by Duncan's New Multiple Range test.

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BIOGRAPHICAL SKETCH

Charles W. Mansfield was born 30 Jan. 1954 in Paducah, Kentucky, and grew up in the Glendale community of rural southern Illinois. After graduating from Pope County High School in 1972, he attended Southern Illinois University at Carbondale where he graduated with a BS in plant and soil science in 1976. He then joined the Peace Corps and went to Colombia, South America, for two and one-half years where he worked as an agriculture extension agent in rural development. While in Colombia he met and married the former Leonor García Flórez. They returned to the U.S. in 1979 and Chuck completed a M.S. degree at the University of Florida in 1981. Upon graduation from the University of Florida, Chuck and his family moved to Marshfield, Missouri, where he worked as an Area Agronomy Specialist for two and one-half years, and then they went back to Colombia. He taught at the Fundación Universitaria de Málaga for two years before returning to the U.S. in 1986 to pursue a Ph.D. program under the supervision of Dr. Jerry Bennett. Chuck is a member of the American Society of Agronomy, the Soil and Crop Science Society of Florida, and Gamma Sigma Delta.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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